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UNIVERSITY OF ALBERTA

THE DYNAMICS OF PLANKTON MODELS WITH NUTRIENT RECYCLING

by

SHIGUI RUAN ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

IN

APPLIED MATHEMATICS

DEPARTMENT OF MATHEMATICS

EDMONTON, ALBERTA
FALL, 1992

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled THE DYNAMICS OF PLANKTON MODELS WITH NUTRIENT RECYCLING submitted by SHIGUI RUAN in partial fulfillment of the degree of Doctor of Philosophy.

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DEDICATED

TO MY FATHER, MY WIFE YILIN

AND MY DAUGHTER MARION

ABSTRACT

In this thesis, we study the dynamics of plankton models with nutrient recycling. We consider both instantaneous and delayed nutrient recycling. The models are represented by ordinary differential equations, reaction-diffusion equations and integrodifferential (delay) equations.

For the two trophic level models with instantaneous nutrient recycling, we consider the question of extinction and persistence. It is also shown that coexistence might occur in the form of bifurcation periodic solutions. Similar results are obtained for a three trophic level model with instantaneous nutrient recycling.

We establish the existence of solutions of the reaction-diffusion models under Dirichlet and Neumann boundary value conditions, respectively. We also discuss the existence and uniqueness of a periodic solution for a reaction-diffusion model with periodi coefficients.

Finally, we show that the delay model with delayed nutrient recycling undergoes a Hopf bifurcation and exhibits uniform persistence.

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CHAPTER 1

INTRODUCTION

An important factor among the many processes which influence ecosystem dynamics is nutrient recycling. The roles of material recycling and energy flow in closed systems where the total nutrient is conserved have been discussed by many authors, c.f. Ulanowicz [28], May [19], Hirata and Fukao [11], Powell and Richerson [23], among others. The effect of material recycling on ecosystem stability and fragility has been studied by Nisbet and Gurney [21] and Nisbet et al. [22], mainly for closed systems. Hallam [9] and Antonios and Hallam [1] studied the role of nutrient recycling on the persistence and extinction of the population of closed communities.

The first attempt to mathematically model profiles of marine plankton was done by Riley et al. [24], who proposed a simple diffusion model to describe the dynamics of plankton. Then models were proposed by Steele [25] which were mainly concerned with phytoplankton-herbivore interactions. The importance of nutrients to the growth of plankton leading to explicit incorporation of nutrient concentrations in the plankton-herbivore models was discussed by Evans and Parslow [7], Taylor [26] and Wroblewski et al. [35]. Recently, Busenberg et al. [5] studied the model constructed by Wroblewski et al. [35], and they showed that under certain conditions the coexistence of phytoplankton and zooplankton occurs in an orbitally stable oscillatory mode. By using center manifold theory, Arnold [2] studied the existence of limit cycles in a predator-prey-nutrient model, and his result suggested that nutrient recycling is an important consideration in the design of phosphorus (nutrient) control strategies.

A natural ecosystem is virtually never totally closed to material fluxes from the outside. These are generally inputs of nutrients to the system, as well as losses from the system. Recently, DeAngelis et al. [6] and Fasham et al. [8] introduced a nutrient input concentration to the plankton models. They also proposed models involving more components of ecosystems. Also in a similar chemostat-like model, Wolkowicz and Lu [30] supposed that the death rates of the components are different.

Models that analyse the spatial distribution of plankton have also been extensively studied. We refer to Riley et al. [24] and Kierstead and Slobodkin [13] for single species models, to Levin and Segel [15], Mimura [20] and Timm and Okubo [27] for two-species models and to Wroblewski [31, 32], Wroblewski and O'Brien [33] and Wroblewski and Richman [34] for models concerning two species feeding on nutrient with nutrient recycling.

In all the papers mentioned previously, the nutrient recycling was considered as an instantaneous term, thus neglecting the time required to regenerate nutrient from dead biomass by bacterial decomposition. In fact, such a delay is always present in a natural system and it increases for decreasing temperature (see Whittaker [29]). Most recently, Beretta et al. [3] and Bischi [4] considered an open system with a single species feeding on a limiting nutrient which is partially recycled after the death of the organisms. They inserted a distributed time delay in the recycling term in order to study its effect on the stability of the positive equilibrium and on resilience.

The purpose of this thesis is to model the dynamics of plankton models with nutrient recycling. We consider both instantaneous and delayed nutrient recycling. The models are represented by ordinary differential equations, reaction diffusion equations and integrodifferential (delay) equations.

This thesis is organized as follows. In Chapter II, we consider three open systems with instantaneous nutrient recycling. The models take into account interaction between phytoplankton, herbivorous zooplankton and dissolved limiting nutrient. In the first model, we introduce a constant input concentration of the limiting nutrient to the system; the washout rates of the components are supposed to be different and the nutrient is partially recycled. We also use a general class of functions to describe nutrient uptake and functional response. We consider the question of extinction and persistence. In the second model, we assume that the nutrient is supplied by a fluctuating input rate, and show that there is an asymptotically stable periodic solution in the N-P plane from which will bifurcate a continuum of positive solutions of the general system and hence coexistence of all populations occur. In the third model, we suppose that the washout rate is periodic. It is shown that coexistence exists for phytoplankton and zooplankton in the form of positive periodic solutions.

A three trophic level food chain model with instantaneous nutrient recycling is considered in Chapter III. Here the dynamics are governed by autotrophic phytoplankton, herbivorous zooplankton, carnivorous zooplankton and dissolved limiting nutrient. Michaelis-Menten functions [35], Ivlev functions [14] and Holling type III response functions [12] are used to describe nutrient uptake and functional responses, respectively. Criteria for one or more or all of the populations to become extinct, i.e., extinction (persistence) thresholds, are derived. It is shown that subject to certain constraints, the system exhibits uniform persistence. By using a theorem in Marsden and McCracken [18], we prove that there is a bifurcation of periodic solutions from one of the coordinate planes into the positive cone.

In Chapter IV, based on the models proposed by Wroblewski et al. [31, 33, 34], we consider three reaction-diffusion plankton models with instantaneous nutrient recycling. By using a semi-group approach (see Henry [10]), we first discuss the global existence of our model under initial and Dirichlet boundary value conditions. For the Neumann boundary value conditions, we establish an existence theorem by means of a comparison principle. Finally, by using a theorem of Liu and Pao [16], we discuss the existence and uniqueness of a periodic solution for the model with periodic coefficients.

A discrete time delay due to gestation and a distributed time delay describing nutrient recycling are inserted into the plankton models in Chapter V. By using the "linear chain trick technique" of MacDonald [17], we transform the two-dimensional integrodifferential system into a three-dimensional one with a discrete time delay. We show that the system undergoes a Hopf bifurcation by choosing the discrete time delay as a bifurcation parameter. The question of persistence of this model is also discussed, and it is shown that both the discrete time delay and the distributed time delay are "harmless" for persistence.

The final chapter contains the concluding discussion and remarks.

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CHAPTER 2

TWO-TROPHIC-LEVEL MODELS

2.1 Introduction

An early attempt to mathematically model profiles of marine plankton by Riley, Stommel and Burrpus [39] has been followed by models varying in complexity. A number of the later models were mainly concerned with phytoplankton-herbivore interactions (see Steele [43]). Recently, Evans and Parslow [17], Taylor [44], Wroblewski, Sarmiento and Flierl [50] constructed models explicitly incorporating nutrient concentrations in the plankton-herbivore models.

The mathematical analysis of plankton models goes back to Hallam [27, 28, 29] who studied stability and persistence properties of a family of non-spatial plankton models, the so-called aquatic ecosystems or nutrient controlled plankton models. In [27], a threshold level for nutrient input required for persistence was given and hence, a necessary and sufficient condition for the persistence of a aquatic ecomodel was obtained. Arnold [1, 2], Arnold and Voss [3] also considered three components models made up of phytoplankton, zooplankton and organic phosphorus nutrient in a lake environment. Certain properties of the models such as the existence of limit cycles were discussed. In [24], Gard provided a simpler and sharper persistence criterion for a zooplankton-phytoplankton-nutrient model with general functional response; he also showed how persistence criteria can be determined for nonautonomous type models in which the nutrient input rate may be time varying. In a recent article, Busenberg et al. [5] studied a model of a zooplankton-phytoplankton-nutrient interaction which was constructed by Wroblewski, Sarmiento and Flierl [50]. It was shown in their paper that under certain conditions the coexistence of phytoplankton and zooplankton occurs in an orbitally stable oscillatory mode.

The zooplankton-phytoplankton-nutrient models describing lakes or oceans are different from the chemostat models (for chemostat models, cf. Waltman [46, 47] and the references therein), since lakes or oceans generally have a residence time of nutrient and sediments measured in years (see Powell and Richerson [37]). Hence the regeneration of nutrient due to bacterial decomposition of the dead biomass must be considered. Nisbet, McKinstry and Gurney [36] studied the effect of material recycling on ecosystem stability for closed systems. We regard nutrient recycling as an instantaneous term, thus neglecting the time required to regenerate nutrient from dead biomass by bacterial decomposition. For delay nutrient recycling in chemostat models, we refer to the recent articles by Beretta, Bischi and Solimano [4], and Freedman and Xu [22].

Phytoplankton death is a gross parameterization of many processes including physiological death, exudation of organic substances and losses of phytoplankton due to sinking of cells through the bottom of the mixed layer (Wroblewski et al. [50]). Cell sinking can be an important loss especially at the end of the spring bloom when nutrients are depleted (Walsh [45]). Also, part of the zooplankton mortality representing the predation on zooplankton by higher predators are not explicitly modelled. The final destination of such dead zooplankton will be either ammonium, fecal pellets, or dead higher predators (Fasham et al. [18]). The fecal pellets and corpses of the higher predators will have high sinking rates and will therefore sink out from the mixed layer. Therefore in models of natural systems washout rate constants (or functions) which describe the removal of biotic components from the systems resulting from washout, harvesting, being buried in deep sediments (DeAngelis et al. [16]), soluble metabolic loss (Evans and Parslow

[17]), or cell sinking (Wroblewski [49], Fasham et al. [18]) must be considered. Global dynamics of a chemostat model with differential death rates was recently studied by Wolkowicz and Lu [48].

In this chapter, we consider three open systems which have three interacting components consisting of phytoplankton (P), herbivorous zooplankton (Z) and dissolved limiting nutrient (N). The two plankton levels are modeled in terms of their nitrogen, phosphorous or silicate content, N, which is assumed to be the nutrient primarily responsible for limiting phytoplankton reproduction.

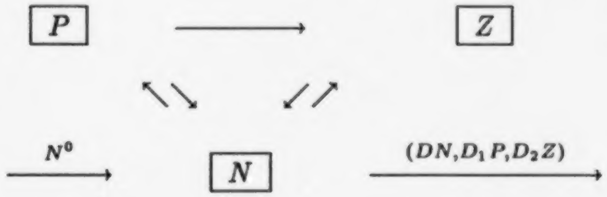

Fig. I The Z-P-N model with constant nutrient input (N^0) and different washout rates $(D, D_1$ and $D_2)$. Arrows indicate nutrient flow pathways between phytoplankton (P), zooplankton (Z) and nutrient (N).

In the first model (Fig. I), based on the model constructed by Wroblewski et al. [50], we introduce a constant input concentration of the limiting nutrient, N^0, different constant washout rates D, D_1 and D_2 for the nutrient, phytoplankton and zooplankton respectively, to the model. We suppose the zooplankton population feeds on both nutrient and phytoplankton (i.e., zooplankton is facultative or obligate), and only part of dead phytoplankton and zooplankton is recycled back into nutrients. We also use a general class of functions to describe nutrient uptake and functional response. Criteria for phytoplankton or zooplankton or both of them to become extinct, i.e., extinction thresholds, are derived. Boundedness of solutions is studied; this is essential for the model to be persistent. Existence of positive equilibria on both the N-P plane and the N-Z plane is considered which demonstrates that for the facultative predator model, the phytoplankton population can survive without zooplankton, and the zooplankton population too, can survive without phytoplankton. It is shown that subject to certain constraints, the system exhibits uniform persistence. In the case where the predator is obligate, we obtain criteria for persistence (and hence coexistence of both zooplankton and phytoplankton).

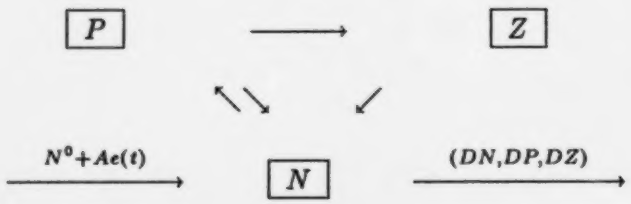

Fig. II The Z-P-N model with periodic nutrient input $(N^0 + Ae(t))$ and constant washout rate (D).

In the second model (Fig. II), we consider the interaction involving nutrient with a periodic input. Similar cases for chemostat models have been studied by Hsu [31], Smith [42], Hale and Somolinos [26], Yang and Freedman [51]. We suppose that zooplankton does not take nutrient directly, i.e., the predator is obligate, and all dead zooplankton and phytoplankton is recycled back into nutrient. This model (as well as the next one) might be more applicable in laboratory aquaria or lakes than in oceanic regions. We show that there is a asymptotically stable periodic solution in the N-P plane, from which will bifurcate a continuum of positive solutions of the general system, hence coexistence of all population may occur.

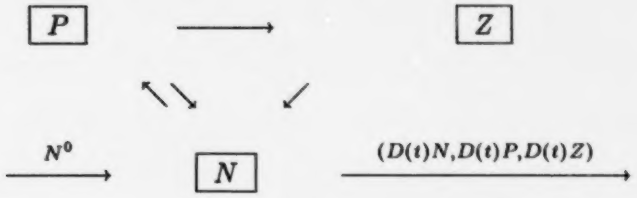

Fig. III The *Z-P-N* model with constant nutrient input (N^0) and periodic washout rate ($D(t)$).

In the third model (Fig. III), we consider the interaction with periodic washout rate (cf. see Butler, Hsu and Waltman [8]). We suppose that the predator is obligate, all phytoplankton ingested by zooplankton is utilized and all dead P and Z is recycled back into the nutrient. It is shown that coexistence exists for phytoplankton and zooplankton in the form of positive periodic solutions.

Persistence in biological systems in a context related to this chapter has been discussed by many authors. We utilize the definitions of persistence developed by Butler, Freedman and Waltman [7], and Butler and Waltman [9], namely if $x(t)$ is such that $x(t) > 0$, we say that $x(t)$ persists if $\liminf_{t\to\infty} x(t) > 0$. Further, we say that $x(t)$ persists uniformly if there exists $\delta > 0$ such that $\liminf_{t\to\infty} x(t) \geq \delta$. Finally, a system persists (uniformly) if all components persist (uniformly).

2.2 An Instantaneous Model

The instantaneous zooplankton-phytoplankton-nutrient (Z-P-N) model consisting of three interacting components, herbivorous zooplankton (Z), phytoplankton (P) and dissolved limiting nutrient (N), is given by the following set of ordinary differential equations

$$\begin{aligned}
\frac{dN}{dt} &= D(N^0 - N) - aPu(N) - bZv(N) + (1-\delta)cZw(P) + \gamma_1 P + \varepsilon_1 Z \\
\frac{dP}{dt} &= aPu(N) - cZw(P) - (\gamma + D_1)P \\
\frac{dZ}{dt} &= Z[bv(N) + \delta cw(P) - (\varepsilon + D_2)].
\end{aligned} \tag{2.1}$$

We assume that all parameters are non-negative and are interpreted as follows:

a – maximal nutrient uptake rate for the phytoplankton

b – maximal nutrient uptake rate for the zooplankton

c – maximal zooplankton ingestion rate

N^0 – input concentration of the nutrient

D – washout rate of the nutrient

D_1 – washout rate of the phytoplankton

D_2 – washout rate of the zooplankton

γ – phytoplankton mortality rate

ε – zooplankton death rate

γ_1 – nutrient recycle rate after the death of the phytoplankton, $\gamma_1 \leq \gamma$

ε_1 – nutrient recycle rate after the death of the zooplankton, $\varepsilon_1 \leq \varepsilon$

δ – the fraction of zooplankton nutrient conversion, $0 < \delta \leq 1$

Functions $u(N)$ and $v(N)$ describe the nutrient uptake rates of phytoplankton and zooplankton, respectively. We assume the following general hypotheses on the nutrient uptake functions (Hale and Somolinos [26]).

(i) The functions are non-negative, increasing and vanish when there is no nutrient.

(ii) There is a saturation effect when the nutrient is very abundant.

That is, we assume that $u(N)$ and $v(N)$ are continuous functions defined on $[0,\infty)$, and satisfy

$$u(0)=0, \qquad \frac{du}{dN}>0 \quad \text{and} \quad \lim_{N\to\infty} u(N)=1, \tag{2.2}$$

$$v(0)=0, \qquad \frac{dv}{dN}>0 \quad \text{and} \quad \lim_{N\to\infty} v(N)=1. \tag{2.3}$$

In particular, these kinds of functions include the Michaelis-Menten functions (Caperon [11], Wroblewski et al. [50], Busenberg et al. [5]),

$$u(N)=\frac{N}{k_1+N}, \qquad v(N)=\frac{N}{k_2+N},$$

where k_1 and k_2 are the half-saturation constants or Michaelis-Menten constants.

$w(P)$ represents the response function describing herbivore grazing. It is also assumed that $w(P)$ is continuous on $[0,\infty)$ and satisfies

$$w(0)=0, \qquad \frac{dw}{dP}>0 \quad \text{and} \quad \lim_{P\to\infty} w(P)=1. \tag{2.4}$$

Usually, Ivlev's functional response formulation [32]

$$w(P)=1-e^{-\lambda P}$$

is used to describe the zooplankton grazing, where λ is the rate at which saturation is achieved with increasing phytoplankton levels (per unit concentration).

We assume that only a fraction of the dead phytoplankton, γ_1 ($\gamma_1 \leq \gamma$), is recycled into dissolved nutrient. The zooplankton dynamics includes growth as assimilated ingested ration and a loss rate of ε due to high level predation, physiological death, etc. Also, we assume that only a fraction, ε_1 $(\varepsilon_1 \leq \varepsilon)$ of the dead zooplankton is recycled into dissolved nutrient within the mixed layer.

During consumption only a fraction of the phytoplankton removed through zooplankton predation, δ $(\delta \leq 1)$, is assumed to be assimilated by zooplankton, the remainder goes directly to the available nitrate.

D, D_1 and D_2 are washout rates (or removal rates, diffusive rates) of biotic components from the system resulting from washout, diffusion, harvesting, being buried in deep sediments, soluble metabolic loss or cell sinking, for example. Those processes in general do not take place at the same time, so we suppose that D, D_1 and D_2 are different.

Note that $E_0 = (N^0, 0, 0)$ is always an equilibrium for system (2.1). We first give criteria for phytoplankton or zooplankton or both of them to become extinct.

Theorem 2.1. *Let the inequality*

$$a \leq \gamma + D_1 \tag{2.5}$$

hold. Then $\lim_{t\to\infty} P(t) = 0$.

Proof: From system (2.1), we have that

$$\begin{aligned}\frac{dP}{dt} &= aPu(N) - cZw(P) - (\gamma + D_1)P \\ &< P[au(N) - (\gamma + D_1)] \\ &\leq P[a - (\gamma + D_1)] \\ &\leq 0 \qquad \text{by (2.5).}\end{aligned}$$

Since there is no invariant set such that $P > 0$ is constant, the theorem follows.

$\square$

Theorem 2.1 demonstrates that if the maximal nutrient uptake rate is less than or equal to the loss rate, then the phytoplankton population is eliminated.

Similarly, we can prove the following theorem.

Theorem 2.2. *Let the inequality*

$$b + \delta c \leq \varepsilon + D_2 \tag{2.6}$$

hold. Then $\lim_{t\to\infty} Z(t) = 0$.

This result shows that the zooplankton population cannot exist if the summation of its maximal nutrient uptake rate and its net ingestion rate is less than or equal to its loss rate.

Corollary 2.3. *If (2.5) and (2.6) hold, then* $\lim_{t\to\infty}\big(N(t), P(t), Z(t)\big) = E_0$.

By Corollary 2.3, if (2.5) and (2.6) hold, then both of the phytoplankton population and zooplankton population become extinct. In this case, it is not feasible for persistence of system (2.1).

If phytoplankton is the top trophic level, and zooplankton is set at zero, then we have the subsystem

$$\begin{aligned} \frac{dN}{dt} &= D(N^0 - N) - aPu(N) + \gamma_1 P \\ \frac{dP}{dt} &= P[au(N) - (\gamma + D_1)]. \end{aligned} \tag{2.7}$$

System (2.7) has an interior equilibrium (N_1, P_1), where

$$N_1 = u^{-1}\left(\frac{\gamma + D_1}{a}\right), \qquad P_1 = \frac{D\big(N^0 - u^{-1}(\frac{\gamma+D_1}{a})\big)}{\gamma + D_1 - \gamma_1}$$

provided

$$\gamma + D_1 < a \tag{2.8}$$

and

$$u^{-1}\left(\frac{\gamma + D_1}{a}\right) < N^0. \tag{2.9}$$

So we have the following theorem.

Theorem 2.4. *If the inequalities (2.8) and (2.9) hold, then system (2.1) has a non-negative equilibrium* $E_1 = (N_1, P_1, 0)$ *where* N_1 *and* P_1 *are defined as above.*

Similarly, we have

Theorem 2.5. *If the inequalities*

$$\varepsilon + D_2 < b \tag{2.10}$$

and

$$v^{-1}\left(\frac{\varepsilon + D_2}{b}\right) < N^0 \tag{2.11}$$

hold, then system (2.1) has a non-negative equilibrium $E_2 = (N_2, 0, Z_2)$ *where*

$$N_2 = v^{-1}\left(\frac{\varepsilon + D_2}{b}\right), \qquad Z_2 = \frac{D\big(N^0 - v^{-1}(\frac{\varepsilon+D_2}{b})\big)}{\varepsilon + D_2 - \varepsilon_1}.$$

Theorem 2.4 indicates that if (2.8) and (2.9) hold, then the phytoplankton population can survive on the nutrient, while Theorem 2.5 demonstrates that the predator zooplankton may be able to survive on the nutrient without the prey phytoplankton if (2.10) and (2.11) hold. This is not true if (2.11) fails, and the equilibrium E_2 does not exist.

Theorem 2.6. *All solutions of system (2.1) are bounded.*

PROOF: We have

$$\begin{aligned}\frac{d}{dt}(N+P+Z) &= DN^0 - DN + \gamma_1 P + \varepsilon_1 Z \\ &\quad - \gamma P - D_1 P - \varepsilon Z - D_2 Z \\ &\leq -D_0(N+P+Z) + DN^0,\end{aligned}$$

where $D_0 = \min\{D, D_1, D_2\}$. The theorem follows. □

Theorem 2.7. *If the non-negative equilibria E_1 and E_2 exist, then (N_1, P_1) and (N_2, Z_2) are globally asymptotically stable in the N-P plane and N-Z plane, respectively.*

PROOF: We only prove the global asymptotic stability of (N_1, P_1) in the N-P plane; the stability of (N_2, P_2) in the N-Z plane can be proved similarly. Define a Liapunov function (c.f. Harrison [30])

$$V(N,P) = \int_{N_1}^{N} \frac{u(x) - u(N_1)}{u(x)}\, dx + \frac{au(N_1) - \gamma_1}{au(N_1)} \int_{P_1}^{P} \frac{x - P_1}{x}\, dx. \qquad (2.12)$$

Then, if (2.8) holds, $u(N_1) - \gamma_1 > 0$, $V(N,P) = 0$ if and only if $N = N_1$, $P = P_1$ and $V(N,P) \geq 0$ in the N-P plane. The time derivative of V along the trajectories of the subsystem (2.6) is

$$\begin{aligned}\frac{dV}{dt} &= \frac{u(N)-u(N_1)}{u(N)}[D(N^0-N)-aPu(N)+\gamma_1 P] \\ &\quad + \frac{au(N_1)-\gamma_1}{au(N_1)}(P-P_1)[au(N)-(\gamma+D_1)] \\ &= \big(u(N)-u(N_1)\big)\left[\frac{D(N^0-N)}{u(N)}-\left(a-\frac{\gamma_1}{u(N)}\right)P-\frac{D(N^0-N_1)}{u(N_1)}+\left(a-\frac{\gamma_1}{u(N_1)}\right)P_1\right] \\ &\quad + \left(a-\frac{\gamma_1}{u(N_1)}\right)(P-P_1)[u(N)-u(N_1)] \\ &= (u(N)-u(N_1))\left[-\frac{D(N^0-N_1)+\gamma_1 P}{u(N)u(N_1)}(u(N)-u(N_1))-\frac{D(N-N_1)}{u(N)}\right] \\ &= -\frac{D(N^0-N_1)+\gamma_1 P}{u(N)u(N_1)}[u(N)-u(N_1)]^2-\frac{D}{u(N)}(N-N_1)\big(u(N)-u(N_1)\big).\end{aligned}$$

Since $N_1 < N^0$, the first term is negative. The second term is negative because $u(N)$ is an increasing function. Thus, $\frac{dV}{dt} \le 0$ and $\frac{dV}{dt} = 0$ if and only if $N = N_1$. The largest invariant subset of the set of the point where $\frac{dV}{dt} = 0$ is (N_1, P_1). Therefore by LaSalle's Theorem (LaSalle and Lefschetz [34]), (N_1, P_1) is globally asymptotically stable. □

Theorem 2.8. *If the inequalities (2.8)–(2.11) hold and*

$$bv(N_1)+\delta cw(P_1)-(\varepsilon+D_2)>0 \tag{2.13}$$

$$au(N_2)-cZ_2w'(0)-(\gamma+D_1)>0, \tag{2.14}$$

then system (2.1) is persistent.

PROOF: By Theorem 2.4 and 2.5, there are three equilibria on all the coordinate planes, i.e., $E_0 = (N^0, 0, 0)$, $E_1 = (N_1, P_1, 0)$ and $E_2 = (N_2, 0, Z_2)$. We first show that all equilibria are saddle points.

For $E_0 = (N^0, 0, 0)$, the variational matrix of system (2.1) at E_0 is

$$\begin{pmatrix} -D & -au(N^0) + \gamma_1 & -bv(N^0) + \varepsilon_1 \\ 0 & au(N^0) - (\gamma + D_1) & 0 \\ 0 & 0 & bv(N^0) - (\varepsilon + D_2) \end{pmatrix}.$$

By inequalities (2.9) and (2.11), the eigenvalues of the variational matrix are $\lambda_1 = -D < 0$, $\lambda_2 = au(N^0) - (\gamma + D_1) > 0$, $\lambda_3 = bv(N^0) - (\varepsilon + D_2) > 0$, so E_0 is a saddle point.

The variational matrix of system (2.1) at $E_1 = (N_1, P_1, 0)$ has the form

$$\begin{pmatrix} -D - aP_1u'(N_1) & -au(N_1) + \gamma_1 & -bv(N_1) + (1-\delta)cw(P_1) + \varepsilon_1 \\ aP_1u'(N_1) & 0 & -cw(P_1) \\ 0 & 0 & bv(N_1) + \delta cw(P_1) - (\varepsilon + D_2) \end{pmatrix},$$

and the eigenvalues of the variational matrix are λ_1, λ_2 which are the roots of the equation

$$\lambda^2 + \big(D + aP_1u'(N_1)\big)\lambda + aP_1u'(N_1)\big(au(N_1) - \gamma_1\big) = 0$$

and

$$\lambda_3 = bv(N_1) + \delta cw(P_1) - (\varepsilon + D_2).$$

Clearly, λ_1 and λ_2 have negative real parts, and $\lambda_3 > 0$ by condition (2.13). Therefore E_1 is a saddle point, and since $\lambda_3 > 0$, E_1 is unstable in the direction orthogonal to the N-P coordinate plane.

The variational matrix of system (2.1) at $E_2 = (N_2, 0, Z_2)$ has the form

$$\begin{pmatrix} -D - bZ_2v'(N_2) & -au(N_2) + (1-\delta)cZ_2w'(0) + \gamma_1 & -bv(N_2) + \varepsilon_1 \\ 0 & au(N_2) - (\gamma + D_1) - cZ_2w'(0) & 0 \\ -bZ_2v'(N_2) & \delta cZ_2w'(0) & 0 \end{pmatrix}.$$

By analogous arguments to those analyzing E_1 and condition (2.14), we can prove that E_2 is a saddle point, and it is unstable in the direction orthogonal to the N-Z coordinate plane.

Now let

$$G(N,P,Z) = au(N) - \frac{cZw(P)}{P} - (\gamma + D_1),$$

$$H(N,P,Z) = bv(N) + \delta cw(P) - (\varepsilon + D_2).$$

We have that

$$H(N_1, P_1, 0) = bv(N_1) + \delta cw(P_1) - (\varepsilon + D_2) > 0$$

$$G(N_2, 0, Z_2) = au(N_2) - cZ_2w'(0) - (\gamma + D_1) > 0.$$

According to Theorem 5.1 of Freedman and Waltman [20], system (2.1) is persistent. This completes the proof. □

Condition (2.13) in Theorem 2.8 means that near the positive equilibrium (N_1, P_1) in the N-P plane, the growth rate of the zooplankton population is positive, and condition (2.14) means that near the positive equilibrium (N_2, Z_2) in the N-Z plane, the growth rate of the phytoplankton population is positive. Theorem 2.8 shows that if inequalities (2.8)–(2.11) hold (which guarantee the existence of (N_1, P_1) and (N_2, Z_2)), then the positive growth rates of zooplankton and phytoplankton near (N_1, P_1) and (N_2, Z_2) respectively, imply the survival of all three components.

In model (2.1), since the predator zooplankton is facultative, competition for the nutrient between phytoplankton and zooplankton exists in some sense, but Theorem 2.8 shows that competitive exclusion does not occur in the Z-P-N models.

Note that from the theorem of Butler, Freedman and Waltman [7] we can obtain uniform persistence for our system. We now are able to state criteria which guarantee the existence of an interior equilibrium, by the corollary of [7].

Theorem 2.9. *Suppose the hypotheses of Theorem 2.8 hold. Then system (2.1) has an interior equilibrium* $E^* = (N^*, P^*, Z^*)$.

As an example, we consider the following model

$$\begin{aligned}
\frac{dN}{dt} &= D(N^0 - N) - \frac{aNP}{k_1 + N} - \frac{bNZ}{k_2 + N} + (1-\delta)cZ(1 - e^{-\lambda P}) + \gamma_1 P + \varepsilon_1 Z \\
\frac{dP}{dt} &= \frac{aNP}{k_1 + N} - cZ(1 - e^{-\lambda P}) - (\gamma + D_1)P \\
\frac{dZ}{dt} &= Z\left[\frac{bN}{k_2 + N} + \delta c(1 - e^{-\lambda P}) - (\varepsilon + D_2)\right]
\end{aligned} \tag{2.15}$$

where all parameters are positive. Now inequalities (2.8) and (2.9) become

$$\frac{\gamma + D_1}{a} < \frac{N^0}{k_1 + N^0}, \tag{2.16}$$

and inequalities (2.10) and (2.12) become

$$\frac{\varepsilon + D_2}{b} < \frac{N^0}{k_2 + N^0}. \tag{2.17}$$

System (2.15) has the following equilibria $E_0 = (N^0, 0, 0)$, $E_1 = (\frac{k_1\alpha}{1-\alpha}, \frac{D(N^0 - \frac{\alpha}{1-\alpha}k_1)}{\gamma + D_1 - \gamma_1}, 0)$ and $E_2 = (\frac{k_2\beta}{1-\beta}, 0, \frac{D(N^0 - \frac{\beta}{1-\beta}k_2)}{\varepsilon + D_2 - \varepsilon_1})$ on the coordinate planes where $\alpha = \frac{\gamma + D_1}{a}$, $\beta = \frac{\varepsilon + D_2}{b}$. By Theorem 2.8, we have

Theorem 2.10. *Suppose inequalities (2.16) and (2.17) hold, if*

$$\frac{k_1\alpha}{k_2 + (k_1 - k_2)\alpha} + \frac{\delta c}{b}\left\{1 - \exp\left[-\frac{\lambda D(N^0 - \frac{\alpha}{1-\alpha}k_1)}{\gamma + D_1 - \gamma_1}\right]\right\} > \beta,$$

$$\frac{k_2\beta}{k_1 + (k_2 - k_1)\beta} - \frac{\frac{c\lambda D}{a}(N^0 - \frac{\beta}{1-\beta}k_2)}{\varepsilon + D_2 - \varepsilon_1} > \alpha.$$

Then system (2.15) is persistent.

In Theorem 2.8, persistence criteria are given when the predator is facultative $(bv(N^0) > \varepsilon + D_2)$; in that case the zooplankton population can survive without the phytoplankton population. Actually, if the predator is obligate $(bv(N^0) < \varepsilon + D_2)$, even though zooplankton cannot survive without phytoplankton, persistence may occur. In the following we consider the case where the predator is obligate.

If we suppose that the zooplankton population does not take nutrient directly, i.e., $b = 0$, then system (2.1) takes the following form

$$\begin{aligned}
\frac{dN}{dt} &= D(N^0 - N) - aPu(N) + (1 - \delta)cZw(P) + \gamma_1 P + \varepsilon_1 Z \\
\frac{dP}{dt} &= aPu(N) - cZw(P) - (\gamma + D_1)P \qquad\qquad (2.18) \\
\frac{dZ}{dt} &= Z[\delta cw(P) - (\varepsilon + D_2)].
\end{aligned}$$

If $\delta c \leq \varepsilon + D_2$, then the zooplankton population cannot exist; if $a \leq \gamma + D_1$, then phytoplankton and hence zooplankton cannot exist. Hence system (2.18) does not persist if any of the above inequalities holds. In the following, we suppose that the inverse direction inequalities, i.e.(2.8) and

$$\varepsilon + D_2 < \delta c \tag{2.19}$$

hold.

Notice that $E_0 = (N^0, 0, 0)$ is an equilibrium for system (2.18) and is globally asymptotically stable in N-axis direction. If (2.8) and (2.9) hold, then $E_1 = (N_1, P_1, 0)$ given by Theorem 2.4 is also an equilibrium of (2.18) and is globally asymptotically stable with respect to the N-P plane. Also all solutions of system (2.18) are bounded.

If (2.9) holds, then E_0 is a saddle point and is unstable in the direction orthogonal to the N-Z plane. If the inequality

$$w(P_1) > \frac{\varepsilon + D_2}{\delta c} \tag{2.20}$$

holds, then E_1 is a saddle point and is unstable in the direction orthogonal to the N-P plane. Hence by Butler-McGehee lemma (c.f. [21]), inequality (2.20) implies the persistence of system (2.18). It is known that persistence of the Z component is equivalent to entire system persistence (Gard and Hallam [25]) for models of the form (2.18). Following the similar arguments by Hallam [27] [28] and Gard [24], we know that condition (2.20) is also necessary for persistence in system (2.18). The result in [7] implies that system (2.18) possesses an interior equilibrium $E^* = (N^*, P^*, Z^*)$ with

$$P^* = w^{-1}\left(\frac{\varepsilon + D_2}{\delta c}\right). \tag{2.21}$$

The above remarks are summarized by the following result:

Theorem 2.11. *Assume (2.8), (2.9) and (2.19) hold. Then system (2.18) persists if and only if (2.20) holds. Furthermore, under (2.20) system (2.18) has a positive interior equilibrium.*

This result indicates that solutions of system (2.18) are uniformly ultimately bounded and have components which do not tend to zero under certain conditions. Condition (2.20) means that near the positive equilibrium (N_1, P_1) in the N-P plane, the growth rate of zooplankton is positive.

Notice also that the right hand side of inequality (2.20) is the value of the function $w(P)$ at P^* by (2.21). So condition (2.20) is equivalent to $w(P_1) > w(P^*)$. Since $w(P)$ is increasing by (2.4), it is also equivalent to $P_1 > P^*$.

Now we consider (2.15) with $b = 0$, $k_1 = k$, namely

$$\begin{aligned} \frac{dN}{dt} &= D(N^0 - N) - \frac{aNP}{k+N} + (1-\delta)cZ(1-e^{-\lambda P}) + \gamma_1 P + \varepsilon_1 Z \\ \frac{dP}{dt} &= \frac{aNP}{k+N} - cZ(1-e^{-\lambda P}) - (\gamma + D_1)P \\ \frac{dZ}{dt} &= Z[\delta c(1-e^{-\lambda P}) - (\varepsilon + D_2)]. \end{aligned} \tag{2.22}$$

System (2.22) has two equilibria on the boundary, $E_0 = (N^0, 0, 0)$ and $E_1 = \left(\frac{\alpha}{1-\alpha}k, \frac{D(N^0 - \frac{\alpha}{1-\alpha}k)}{\gamma + D_1 - \gamma_1}, 0\right)$ provided (2.16) holds, where $\alpha = \frac{\gamma + D_1}{a}$. The persistence condition (2.20) becomes

$$1 - \exp\left[-\frac{\lambda D(N^0 - \frac{\alpha}{1-\alpha}k)}{\gamma + D_1 - \gamma_1}\right] > \frac{\varepsilon + D_2}{\delta c} \tag{2.23}$$

and the positive interior equilibrium $E^* = (N^*, P^*, Z^*)$ is given by

$$P^* = \frac{1}{\lambda} \ln \frac{\delta c}{\delta c - (\varepsilon + D_2)},$$

$$Z^* = \frac{\delta P^*}{\varepsilon + D_2} \left[a \frac{N^*}{k + N^*} - (\gamma + D_1) \right],$$

and N^* is the positive root of

$$DN^{*2} + BN^* - C = 0, \tag{2.24}$$

where

$$B = D(k - N^0) + \left[(\gamma + D_1 - \gamma_1) + \delta(a - \gamma - D_1) \left(1 - \frac{\varepsilon_1}{\varepsilon + D_2} \right) \right] P^*,$$

$$C = k \left\{ DN^0 + \left[\delta(\gamma + D_1) \left(1 - \frac{\varepsilon_1}{\varepsilon + D_2} \right) - (\gamma + D_1 - \gamma_1) \right] P^* \right\}.$$

Therefore, we have the following result.

Theorem 2.12. *If (2.16) and (2.19) hold, then system (2.22) persists if and only if (2.23) holds. Furthermore, under (2.23), system (2.22) has a unique positive interior equilibrium* $E^* = (N^*, P^*, Z^*)$ *where* N^*, P^* *and* Z^* *are defined as above.*

For the Michaelis-Menten function $u(N) = \frac{N}{k+N}$ and the Ivlev function $w(P) = 1 - e^{-\lambda P}$, we proved in Theorem 2.12 that system (2.22) has a unique positive interior equilibrium; we conjecture uniqueness is also true in Theorem 2.11 and Theorem 2.8.

The numerical analysis by Busenberg et al. [5] is very interesting. Using the parameter values reported by Wroblewski et al. [50],

$$a = 2.0, \qquad k = 0.2 \qquad \gamma = 0.1, \qquad \varepsilon = 0.2,$$

$$\lambda = 0.5, \qquad c = 0.5, \qquad \delta = 0.7,$$

they showed numerically that for a special case of our model (2.22) when $D = D_1 = D_2 = 0$, $\gamma_1 = \gamma$, $\varepsilon_1 = \varepsilon$, there is a periodic oscillatory coexistence state.

For our model (2.22), if we use the above parameter values reported by Wroblewski et al. and the following values

$$D = 0.4, \qquad D_1 = 0.3, \qquad D_2 = 0.1,$$

$$N^0 = 3.75, \qquad \gamma_1 = 0.08, \qquad \varepsilon_1 = 0.15,$$

then all conditions of Theorem 1.12 are satisfied, hence system (2.22) with the above parameter values is persistent, and has a unique positive interior equilibrium $E^* = (0.38, 3.89, 8.17)$ which is unstable.

2.3 A Model for Fluctuating Nutrient Input

To simulate seasons or day/night cycles in a natural environment, we assume that the input concentration of the limiting nutrient is allowed to vary periodically around a mean value $N^0 > 0$, with an amplitude A, $A < N^0$, and period τ; that is, according to the law $N^0 + Ae(t)$, where $e(t)$ is a τ-periodic function of mean value zero and $|e(t)| \leq 1$. Though the following technique works for the case when the predator is facultative, a mathematical simplification arises if we assume that the predator is obligate, i.e., $b = 0$. We also assume that $\gamma_1 = \gamma$, $\varepsilon_1 = \varepsilon$

and $D = D_1 = D_2$; the latter assumption often appears in chemostat models (c.f. Waltman [47]).

We consider the Z-P-N model with periodic nutrient input

$$\begin{aligned}\frac{dN}{dt} &= D(N^0 + Ae(t) - N) - aPu(N) + (1-\delta)cZw(P) + \gamma P + \varepsilon Z \\ \frac{dP}{dt} &= aPu(N) - cZw(P) - (\gamma + D)P \\ \frac{dZ}{dt} &= Z[\delta cw(P) - (\varepsilon + D)],\end{aligned} \tag{3.1}$$

where functions $u(N)$ and $w(P)$, parameters D, N^0, a, c, δ, γ and ε are the same as in Section 2.

This system describes conditions for plankton growth in lakes where the limiting nutrients such as silica nitrate and phosphate are supplied from streams draining the watershed. As seasons change, stream drainage patterns change causing variations in the supply of nutrients.

Let $N^*(t)$ be the unique τ-periodic solution of the equation

$$\frac{dN}{dt} = -DN + D(N^0 + Ae(t)), \tag{3.2}$$

that is,

$$N^*(t) = \frac{D}{e^{D\tau} - 1} \int_0^\tau e^{Dr}(N^0 + Ae(t+r))\, dr. \tag{3.3}$$

It is easy to verify that $N^*(t)$ is globally exponentially stable, and moreover, every solution $N(t)$ of (3.2) can be written as

$$N(t) = N^*(t) + Ce^{-Dt},$$

where $C = N(0) - N^*(0)$. Suppose

$$e_1 = \min_{0 \le t \le \tau} e(t), \qquad e_2 = \max_{0 \le t \le \tau} e(t).$$

Then all solutions $N(t)$ eventually enter the interval $[N^0 + Ae_1, N^0 + Ae_2]$ and remain there for all future time.

Definition 3.1 A system of ordinary differential equations $\frac{dy}{dt} = f(t, y)$ defined in a domain Ω is ***dissipative*** if there exists a B such that all solutions $y(t)$ with $y(t) \in \Omega$ for all t satisfy $\limsup_{t \to \infty} |y(t)| \le B$.

Theorem 3.2. *Each solution $(N(t), P(t), Z(t))$ of system (3.1) with initial value in R^3_+ will remain in R^3_+ for all $t \ge 0$, and the system is dissipative in R^3_+.*

PROOF: It is obvious that solutions $(N(t), P(t), Z(t))$ of (3.1) with initial data (N_0, P_0, Z_0) in R^3_+ remain in R^3_+ for all $t \ge 0$. Let

$$S(t) = N(t) + P(t) + Z(t) - N^*(t). \tag{3.4}$$

We have that

$$\frac{dS}{dt} = -DN - DP - DZ + DN^* = -DS.$$

It follows that for some B_1 and $t \ge 0$,

$$S(t) = S(0)e^{-Dt} \le B_1.$$

Thus, for $t \ge 0$

$$N(t) + P(t) + Z(t) \le N^*(t) + B_1.$$

Since $N^*(t)$ is a globally exponentially stable periodic solution of (3.2), there is a B such that

$$\limsup_{t \to \infty} [N(t) + P(t) + Z(t)] \leq B, \tag{3.5}$$

that is, system (3.1) is dissipative in R^3. ☐

We know that in an Euclidean space $\mathcal{E}$, a periodic ordinary differential equation is equivalent to a dynamical system $\pi(x,t)$ on a cylinder $E = \mathcal{E} \times \mathcal{Q}$ with a flow $\mathcal{F}$, where $\mathcal{Q} = [0,\tau]/\{0,\tau\}$ is a quotient space of $[0,\tau]$ by identifying 0 and τ, or $\mathcal{Q}$ can be regarded as a nontrivial circle on the plane. We think of E as a subset of $\mathcal{E} \times R^2$. In fact, for system (3.1), $\mathcal{E} = R \times R^3_+$. To study the asymptotic behavior of solutions of (3.1), we only need to study the Ω-limit sets of trajectories of a dynamical system π with flow $\mathcal{F}$ on E.

For each point $x \in E$, we denote it by $x = (N, P, Z, Q)$, where $Q \in \mathcal{Q}$. Let $\partial E_P = \{(N,P,Z,Q) \in E \mid P = 0\}$, $\partial E_Z = \{(N,P,Z,Q) \in E \mid Z = 0\}$. We denote the restrictions of flow $\mathcal{F}$ to ∂E_P and ∂E_Z by $\partial \mathcal{F}_P$ and $\partial \mathcal{F}_Z$, respectively. $\Lambda^+(x)$ denotes the omega limit set of the orbit through x.

Definition 3.3 *An isolated invariant set* M for the flow $\mathcal{F}$ is a nonempty invariant set which is the maximal invariant set in some neighbourhood of itself. Note that if M is a compact, isolated invariant set, one may always choose a compact isolating neighbourhood.

For an isolated invariant set $M \subset E$, we define

$$W_w^+(M) = \{x \in E \mid \Lambda^+(x) \cap M \neq \emptyset\}$$

as the *weak stable set* and

$$W^+(M) = \{x \in E \mid \Lambda^+(x) \neq \emptyset \quad \text{and} \quad \Lambda^+(x) \subset M\}$$

as the *stable set*, and we denote

$$\Omega(M) = \bigcup_{x \in M} \Lambda^+(x).$$

Define $M = \{(N^*(t), 0, 0, Q) \in E \mid Q \in \mathcal{Q}\}$, then M is a compact invariant set for $\mathcal{F}$. It is easy to verify that the boundaries ∂E_P, ∂E_Z and hence $\partial E = \partial E_P \cup \partial E_Z$ are invariant. Moreover, we have

Lemma 3.4. *$\partial E_P \subset W^+(M)$ such that if $x \in \partial E_P \setminus M$, then*

$$\|\pi(x,t)\| \to \infty \quad \text{as} \quad t \to -\infty.$$

PROOF: Since $Z(t) = Z(0)e^{-(\epsilon+D)t}$ whenever $x = (N_0, 0, Z_0, 0) \in \partial E_P$, we have $\pi(x,t) = (N(t), 0, Z(t), t \mod (\tau)) \to (N^*(Q(t)), 0, 0, Q(t))$ as $t \to \infty$, $Q \in [0,\tau]$, i.e., $\partial E_P \subset W^+(E)$. On the other hand, for $x \in \partial E_P \setminus M$, since $N(t) = N^*(t) + Ce^{-Dt}$ for some constant $C \neq 0$ whenever $N(t_0) \neq N^*(t_0)$ for any $t_0 \in [0,\tau]$, then $N(t) \neq N^*(t)$. Therefore $\|\pi(x,t)\| \to \infty$ as $t \to -\infty$.

□

Let $B(\tau)$ denote the Banach space of continuous τ-periodic real valued functions $x : R \to R$ under the supremum norm

$$|x|_0 = \sup_{0 \leq t \leq \tau} |x(t)|.$$

Let $B_+(\tau) = \{x \in B(\tau) \mid x(t) > 0 \text{ for all } t\}$ and

$$\langle x(t) \rangle = \frac{1}{\tau} \int_0^\tau x(t)\, dt.$$

The following result indicates that if the phytoplankton population has positive growth rate near the stable periodic solution $N^*(t)$ of (3.2), then it is persistent.

Theorem 3.5. *If*

$$\sigma_0 = a\langle u(N^*(t)) \rangle - (\gamma + D) > 0, \tag{3.6}$$

then

$$\liminf_{t \to \infty} P(t) > 0.$$

PROOF: First we prove that M is isolated. Since $\sigma_0 > 0$ and $u(N)$ is continuous, there is $\Delta_0 > 0$ such that for some $\alpha > 0$

$$a\langle u(N^*(t+\alpha) - \Delta_0) \rangle - (\gamma + D + \Delta_0) \geq \frac{\sigma_0}{2} > 0. \tag{3.7}$$

Since $\mathcal{F}$ is dissipative, we can find $\xi > 0$ and $t_0 \geq 0$ such that $0 \leq P(t) \leq \xi$ for all $t \geq t_0$. Define

$$L = c \max_{0 \leq P(t) \leq \xi} w(P) > 0 \qquad \text{and} \qquad \Delta = \frac{\Delta_0}{L} > 0.$$

Then $\mathcal{N}_\Delta = \{x \in E \mid \rho(x, M) < \Delta\}$ is an isolating neighbourhood of M, where ρ is the metric of E. Otherwise, there is an invariant set G containing M in $\mathcal{N}_\Delta$ with $G \setminus M \neq \emptyset$. Lemma 3.3 implies that $(G \setminus M) \cap \partial E_P = \emptyset$. Therefore for any $x \in G \setminus M$, then $x \notin \partial E_P$, i.e., $P_0 > 0$. Since G is invariant, $\gamma^+(x) \subset G \subset \mathcal{N}_\Delta$ where $\gamma^+(x)$ is the positive semiorbit through x. Now we have

$$\frac{d}{dt}[\ln P(t)] \geq au(N^*(t) - \Delta_0) - (\gamma + D + \Delta_0) \quad \text{in } \mathcal{N}_\Delta.$$

From (3.7) it follows that

$$P(n\tau) \geq P_0 \exp\left(\frac{\sigma_0}{2} n\tau\right) \to \infty \quad \text{as } n \to \infty,$$

a contradiction to $\pi(x, n\tau) \in G$ for all $n \geq 0$. So M is isolated.

Now for any $x \in E$ and $\pi(x,t) = \big(N_x(t), P_x(t), Z_x(t), t \mod(\tau)\big)$, if $\liminf_{t\to\infty} P_x(t) = 0$, then $\Lambda^+(x) \cap \partial E_P \neq \emptyset$, and hence $M \subset \Lambda^+(x)$, so $W_w^+(M) = \{x \in E \mid \liminf_{t\to\infty} P_x(t) = 0\}$. We claim that for any $x \in E \setminus \partial E_P$, if $\Lambda^+(x) \in M$, then there exists $\alpha > 0$ such that

$$|N_x(t) - N^*(t+\alpha)| \to 0 \quad \text{as } t \to \infty.$$

In fact, if $\Lambda^+(x) \subset M$, then $P_x(t)$ and $Z_x(t)$ tend to zero as $t \to \infty$, which implies $N_x(t) - N^*(t+\alpha)$ tends to zero for some $\alpha > 0$. Hence

$$\lim_{t\to\infty}[a\langle u(N(t))\rangle - (\gamma + D)] = \sigma_0 > 0$$

and $\liminf_{t\to\infty} P_x(t) > 0$, a contradiction to $\Lambda^+(x) \cap \partial E_P \neq \emptyset$, i.e., $x \notin W^+(M)$, by Lemma 3.4 we have $W^+(M) = \partial E_P$, so $x \in W_w^+(M) \setminus W^+(M)$. Hence by Theorem 4.1 of Butler and Waltman [9], $\Lambda^+(x) \cap (W^+(M) \setminus M) \neq \emptyset$. It follows from Lemma 3.4 that $\Lambda^+(x)$ is unbounded, a contradiction to the dissipativeness of $\mathcal{F}$. Hence $\Lambda^+(x) \cap \partial E_P = \emptyset$, and $\Lambda^+(x)$ is compact, so $\rho(\Lambda^+(x), \partial E_P) > 0$, i.e., $\liminf_{t\to\infty} P(t) > 0$. □

Theorem 3.6. *If* $\sigma_0 > 0$, *then there exists a nontrivial asymptotically stable* τ*-periodic orbit on* ∂E_Z.

PROOF: Define a Poincaré map T from P-Z plane to itself by $T(N_0, P_0) = (N(\tau), P(\tau))$. By Theorem 3.5 and the dissipativity for each (N_0, P_0) in the interior of R^2_+, $\{T^n(N_0, P_0)\}$ has a convergent subsequence. So by Massera's fixed point theorem (see Sansone and Conti [41]), there exists a fixed point $(\overline{N}, \overline{P})$ of T in the interior of R^2_+, which gives a nontrivial periodic orbit on ∂E_Z.

We observe that $v(N, P, t) = N + P$ is a solution of the initial-boundary value problem

$$\left\{\begin{aligned} & v_t + [D(N^0 + Ae(t) - N) - (au(N) - \gamma)P]v_N \\ & \qquad\qquad + [(au(N) - (\gamma + D)P]u_P + Du = D(N^0 + Ae(t)) \\ & v(N, 0, t) = N^*(t), \quad v(N, P, 0) = v(N, P, \tau), \quad t \in [0, \tau],\ N \geq 0,\ P \geq 0. \end{aligned}\right.$$

By Theorem 3.7 and 3.8 of Yang and Freedman [51], the nontrivial τ-periodic orbit on ∂E_Z is asymptotically stable. This completes the proof. ☐

Let $(\overline{N}, \overline{P})$ be the asymptotically stable τ-periodic solution of the reduced system

$$\begin{aligned} \frac{dN}{dt} &= D(N^0 + Ae(t) - N) - aPu(N) + \gamma P \\ \frac{dP}{dt} &= P[au(N) - (\gamma + D)] \end{aligned} \tag{3.8}$$

in Theorem 3.6. We will show in the following that this solution of (3.8) yields a solution $(N, P, Z) = (\overline{N}, \overline{P}, 0) \in B^3_+(\tau)$ of system (3.1) from which will bifurcate a continuum of positive solutions of (3.1) using ε as the bifurcating parameter.

To do this by means of Theorem 1 of Cushing [14], it is necessary that the solution $(\overline{N}, \overline{P})$ of the reduced system (3.8) be *noncritical*; i.e., that the linearized system of (3.8) at $(\overline{N}, \overline{P})$ have no Floquet exponents with zero real part. We assume throughout that $(\overline{N}, \overline{P})$ is stably noncritical, i.e., that these Floquet exponents have negative real parts.

Theorem 3.7. *Assume* $\sigma_0 > 0$ *and that* $(\overline{N}, \overline{P}) \in B^2_+(\tau)$ *is a stably noncritical solution of (3.8). Then there exists a set* $\Pi^+ = \{(N, P, Z, \mu) \in B^3_+(\tau) \times R\}$ *with* $(N, P, Z) > 0$ *solving (3.1), the closure of* Π^+ *is a continuum which connects* $(\overline{N}, \overline{P}, 0, \overline{\mu}) \in B^3(\tau) \times R$, $\overline{\mu} = -\langle cw(\overline{P})\rangle$, *to a solution of the form* $(\widetilde{N}, \widetilde{P}, 0, \widetilde{\mu}) \in B^3(\tau) \times R$, *where* $(\widetilde{N}, \widetilde{P}, 0, \widetilde{\mu}) \neq (\overline{N}, \overline{P}, 0, \overline{\mu})$, $\widetilde{N} > 0$ *and* $\widetilde{P} > 0$.

PROOF: Define $\Omega^3 = \{(N, P, Z) \in R^3 \mid N > 0\}$, by Theorem 1 of Cushing [14] with $d_2(t) = -\mu = -(\varepsilon + D)$, there is a continuum $C^+ \subset B^3(\tau) \times R$ of solutions of (3.1) which contains the bifurcating point $(\overline{N}, \overline{P}, 0, \overline{\mu})$ and which connects to the boundary of the set $\Omega^3_\tau \times R \subset B^3(\tau) \times R$, where $\Omega^3_\tau = \{(N, P, Z) \in B^3(\tau) \mid N + \overline{N} > 0\}$. And in an open neighborhood of $(\overline{N}, \overline{P}, 0, \overline{\mu})$, the set $C^+/\{(\overline{N}, \overline{P}, 0, \overline{\mu})\}$ consists of positive solutions of (3.1). The continuum C^+ cannot consist entirely of positive solutions, otherwise, in order to connect to the boundary of $\Omega^3_\tau \times R$, C^+ would have to be unbounded which would contradict Theorem 3.2. Thus C^+ must leave the positive cone $B^3_+(\tau) \times R$ at a point other than the bifurcating point.

Denote by C^+_0 the maximal subcontinuum of C^+ which connects $(\overline{N}, \overline{P}, 0, \overline{\mu})$ to the boundary of $B^3_+(\tau) \times R$ and define $\Pi^+ = C^+_0 \cap (B^3_+(\tau) \times R)$. Then the closure of Π^+ is a continuum which connects $(\overline{N}, \overline{P}, 0, \overline{\mu})$ to the boundary of $B^3_+(\tau) \times R$, i.e., the closure of Π^+ contains $(\overline{N}, \overline{P}, 0, \overline{\mu})$ and a point $(\widetilde{N}, \widetilde{P}, 0, \widetilde{\mu}) \neq (\overline{N}, \overline{P}, 0, \overline{\mu})$ where $\widetilde{N} \geq 0$ and $\widetilde{P} \geq 0$.

Let $(N_n, P_n, 0, \mu_n) \in \Pi^+$ be a sequence which converges in $B^3(\tau) \times R$ to $(\widetilde{N}, \widetilde{P}, 0, \widetilde{\mu})$. If $(N, P, Z) = (\widetilde{N}, \widetilde{P}, 0)$, dividing the second equation of (3.1) by $P_n > 0$ and taking average, we obtain

$$\langle au(N_n) \rangle = \gamma + D. \tag{3.9}$$

If $\widetilde{N} \equiv 0$, let $n \to \infty$ in (3.9), then we get a contradiction to $\gamma + D > 0$. Hence it must be the case $\widetilde{N} > 0$.

If $\widetilde{P} \equiv 0$, then from the first equation of (3.1) in the limit as $n \to \infty$, we see that $\widetilde{N} \in B_+(\tau)$ solves the periodic equation (3.2) and hence $\widetilde{N} = N^*$. From (3.9), it follows that $\langle au(N^*) \rangle = \gamma + D$, a contradiction to $\sigma_0 > 0$. Hence $\widetilde{N} > 0$ and $\widetilde{P} > 0$. ☐

Since $\sigma_0 > 0$ is the persistence condition for the phytoplankton population by Theorem 3.5, Theorem 3.7 demonstrates that coexistence of all components could occur if phytoplankton is persistent and if the death rate of zooplankton is reasonably low. This is reminiscent of a similar phenomena for the chemostat models in a periodic environment studied by Smith [42] and Cushing [15]. For the Michaelis-Menten function $u(N) = \frac{N}{k+N}$ and the Ivlev function $w(P) = 1 - e^{-\lambda P}$, one can determine the stability of the bifurcating solutions in Theorem 3.7, following the procedures by Smith [42], Cushing [15] or Keener [33].

2.4 A Model for Fluctuating Nutrient Input

Consider the zooplankton-phytoplankton-nutrient model with periodic washout rate

$$
\begin{aligned}
\frac{dN}{dt} &= D(t)(N^0 - N) - aPu(N) + \gamma P + \varepsilon Z \\
\frac{dP}{dt} &= aPu(N) - cZw(P) - (\gamma + D(t))P \\
\frac{dZ}{dt} &= Z\left[cw(P) - (\varepsilon + D(t))\right],
\end{aligned}
\tag{4.1}
$$

where the periodic washout rate $D(t)$ is a positive, continuous function with period τ, all parameters and other functions are same as in Section 2. It is convenient to scale time by the mean value of $D(t)$, i.e.,

$$\langle D(t)\rangle = \frac{1}{\tau}\int_0^\tau D(t)\,dt.$$

We assume that all the phytoplankton removed through zooplankton predation is assimilated by zooplankton, and all dead phytoplankton and zooplankton are recycled to nutrient completely, i.e., $\delta = 1$, $\gamma_1 = \gamma$, $\varepsilon_1 = \varepsilon$. Similar to the procedure in Section 3, we know that the positive cone and the boundaries ∂E_P, ∂E_Z are invariant, and the system is dissipative, i.e., we have

$$\lim_{t\to\infty}[N(t) + P(t) + Z(t)] = N^0,$$

where the convergence is exponential.

Firstly we consider the two dimensional system

$$
\begin{aligned}
\frac{dN}{dt} &= D(t)(N^0 - N) - aPu(N) + \gamma P \\
\frac{dP}{dt} &= P[au(N) - (\gamma + D(t))].
\end{aligned}
\tag{4.2}
$$

For any solution of (4.2), $N(t) + P(t) = N^0 + R(t)$ where $R(t) = O(e^{-\alpha t})$ as

$t \to \infty$ for some $\alpha > 0$. Then $P(t)$ is a solution of

$$\frac{dx(t)}{dt} = x(t)\big[au(N^0 - x(t)) - (\gamma + D(t))\big] + r(t), \tag{4.3}$$

where $r(t) = O(e^{-\alpha t})$ as $t \to \infty$ and $\alpha > 0$. In turn, (4.3) is a perturbation of

$$\frac{dy(t)}{dt} = y(t)\big[au(N^0 - y(t)) - (\gamma + D(t))\big]. \tag{4.4}$$

It was shown by Butler and Freedman [6] using Massera's theorem that equation (4.4) has a unique positive τ-periodic solution $\varphi(t)$ which is globally asymptotically stable. It is not difficult to show that $\varphi(t)$ is exponentially asymptotically stable. A simple Gronwall's inequality argument shows that if $x(t)$ is any solution of (4.3), then $x(t) = \varphi(t) + O(e^{-\beta t})$ for some $\beta > 0$. Note that $\varphi(t)$ is independent of the choice of $P(t)$, although (4.3) is not; in particular, $P(t)$ converges exponentially to $\varphi(t)$ as $t \to \infty$. Define $\psi(t) = N^0 - \varphi(t)$. Then $N(t)$ converges exponentially to $\psi(t)$ as $t \to \infty$. And

$$\begin{aligned}
\frac{d\varphi(t)}{dt} &= \varphi(t)\big[au(N^0 - \varphi(t)) - (\gamma + D(t))\big] = \varphi(t)\big[au(\psi(t)) - (\gamma + D(t))\big], \\
\frac{d\psi(t)}{dt} &= -\frac{d\varphi(t)}{dt} = -a\varphi(t)u(\psi(t)) + (N^0 - \psi(t))(\gamma + D(t)).
\end{aligned}$$

Thus $(\psi(t), \varphi(t))$ is a solution of (4.2) and is globally exponentially stable.

Referring back to Theorems 2.1 and 2.2, since $\langle D \rangle = 1$ we need $a > \gamma + 1$ and $c > \varepsilon + 1$. Hence we have the following result.

Theorem 4.1. *Assume that $a > \gamma + 1$. There are positive τ-periodic functions $N(t)$ and $\varphi(t)$, such that the solution $(N(t), \varphi(t))$ of (4.2) is exponentially stable for (4.2), and $\varphi(t)$ is globally asymptotically stable for (4.4).*

Now for the three dimensional system (4.1), there may be two periodic solutions on the boundary of the nonnegative cone, the constant solution $E_0 = (N^0, 0, 0)$ and solution $E_1 = (N(t), \varphi(t), 0)$.

Our main purpose in this section is to prove the following theorem.

Theorem 4.2. *Let* a *and* γ *be given such that* $a > \gamma + 1$. *If there exists* $\alpha = \alpha(a, \gamma)$ *such that for any* $c > \alpha$, *the bifurcation parameter* ε *can be chosen such that* $\langle w(\varphi(t)) \rangle > \frac{\varepsilon+1}{c}$, *where* $\varphi(t)$ *is the positive* τ*-periodic solution of (4.4), then system (4.1) possesses a positive* τ*-periodic solution* $(N(t), P(t), Z(t))$ *near* E_1 *and bifurcating from* E_1.

PROOF: We may restrict our attention to the invariant triangle $\Delta : N + P + Z = N_0, \quad N, P, Z \geq 0$. Eliminating N from (4.1) restricted to Δ, we have the equations

$$\begin{aligned} \frac{dx_1}{dt} &= x_1 f_1(t, x_1, x_2) \\ \frac{dx_2}{dt} &= x_2 f_2(t, x_1, x_2), \end{aligned} \tag{4.5}$$

where

$$\begin{aligned} f_1(t, x_1, x_2) &= au(N^0 - x_1 - x_2) - cx_2 \frac{w(x_1)}{x_1} - (\gamma + D(t)), \\ f_2(t, x_1, x_2) &= cw(x_1) - (\varepsilon + D(t)). \end{aligned}$$

System (4.5) is a predator-prey model with periodic coefficients. We verify that conditions of Theorem 2.2 of Butler and Freedman [6] are satisfied.

(H_1) $\quad f_{11} = \frac{\partial f_1}{\partial x_1} = -au' - cx_2 \frac{w'(x_1)}{x_1} + cx_2 \frac{w(x_1)}{x_1},$

$\quad f_{12} = \frac{\partial f_1}{\partial x_2} = -au' - c\frac{w(x_1)}{x_1}, \quad f_{21} = \frac{\partial f_2}{\partial x_1} = cw'(x_1), \quad f_{22} = \frac{\partial f_2}{\partial x_2} = 0.$

Hence f_{ij} $(i,j=1,2)$ exist and are continuous for $(t,x_1,x_2)\in R\times R^2_+$, where $R^2_+=\{(x_1,x_2)\in R^2,\ x_1\geq 0,\ x_2\geq 0\}$.

(H_2) In the absence of predator, there is a seasonally varying carrying capacity for the prey, say the function $K_1^*(t)$, such that $[x_1-K_1^*(t)]f_1(t,x_1,0)=[x_1-K_1^*(t)][au(N^0-x_1)-(\gamma+D(t))]<0$ for all $x_1>0$ and $x_1\neq K_1^*(t)$.

(H_3) There exists a critical population density for the predator, say $K_2^*(t)$, above which it cannot survive in the absence of prey, such that $[x_2-K_2^*(t)]f_1(t,0,x_2)=[x_2-K_2^*(t)][au(N^0-x_2)-cx_2w'(0)-(\gamma+D(t)]<0$ for all $x_2\geq 0$ and $x_2\neq K_2^*(t)$.

(H_4) $f_{12}=-au'-c\frac{w(x_1)}{x_1}<0$ for all $(t,x_1,x_2)\in R\times R^2_+$.

(H_5) $x_1f_{11}+x_2f_{22}=-a(x_1+x_2)u'-cx_2w'(x_1)<0$ for all $(t,x_1,x_2)\in R\times R^2_+$.

(H_6) There is a minimum level for the prey population, say $\hat{K}_1(t)$, at which the predator can survive when its own population density is at a low level, this $\hat{K}_1(t)$ is such that $[x_1-\hat{K}_1(t)]f_2(t,x_1,0)=[x_1-\hat{K}_1(t)][cw(x_1)-(\varepsilon+D(t))]>0$ for all $x_1\geq 0$ and $x_1\neq\hat{K}_1(t)$.

(H_7) $f_{22}=0$ for all $(t,x_1,x_2)\in R\times R^2_+$.

(H_8) $x_1f_{21}+x_2f_{22}=cx_1w'(x_1)>0$ for all $(t,x_1,x_2)\in R\times R^2_+$.

And we have

$$\langle f_2(t,0,0)\rangle=\langle-(\varepsilon+D(t))\rangle=-\varepsilon-1\leq 0,$$
$$\langle f_2(t,\varphi(t),0)\rangle=\langle cw(\varphi(t))\rangle-(\varepsilon+D(t))=c\langle w(\varphi(t))\rangle-(\varepsilon+1)>0.$$

By Theorem 2.2 of Butler and Freedman [6], system (4.5) has a periodic solution $(\psi_1(t),\psi_2(t))$ with $\psi_1(t)>0$ and $\psi_2(t)>0$. As in [6], $\langle f_2(t,0,0)\rangle=-\varepsilon-1$, so ε can be chosen as a bifurcation parameter such that system (4.1) has a positive τ-periodic solution $(N(t),P(t),Z(t))$ near E_1 and which bifurcates from E_1.

This completes the proof. □

This result indicates that if the growth rate of phytoplankton is positive and the death rate of zooplankton is relatively low, then a positive periodic solution in the three dimensional space will bifurcate from the asymptotically stable periodic solution in the $N-P$ plane, hence predator-prey coexistence could occur.

2.5 Discussion

In this chapter we have discussed several zooplankton-phytoplankton-nutrient models with general nutrient uptake functions and instantaneous nutrient recycling terms. Different from the model studied by Wroblewski et al. [50] and Busenberg et al. [5], we introduce nutrient concentration input and washout rates to the plankton-nutrient interacting models.

Firstly, we have considered a model with a constant nutrient input and different constant washout rates, the zooplankton population could be facultative or obligate. We have given conditions for boundedness of solutions, existence and stability of the equilibria and persistent criteria for the system. Competition for the nutrient exists in some sense if zooplankton is facultative, but competitive exclusion does not happen. For the case where zooplankton is obligate, persistence has been studied.

As a consequence of the persistence Theorem 2.11, we note that model (2.18) has a dynamic persistence threshold; that is, there exists a number above which the system persists, below which it does not. From persistence condition (2.20) we get the non-dimensional persistence threshold in terms of the nutrient input concentration

$$N^0 > u^{-1}\left(\frac{\gamma + D_1}{a}\right) + \frac{\gamma + D_1 - \gamma_1}{D} w^{-1}\left(\frac{\varepsilon + D_2}{\delta c}\right). \tag{5.1}$$

This inequality demonstrates that the model is nutrient controlled (Hallam [28]). Persistence occurs more likely if the nutrient input concentration (N^0) is increased or the death rate of the zooplankton population (ε) is relatively low. Since enriching the environment may destabilize the system, that is, "enrichment paradox" may happen (see Busenberg et al. [5], also Ruan and Freedman [40] and Freedman and Ruan [20]), it is natural to seek oscillatory coexistence of all components.

Next we have considered the plankton-nutrient interacting models with periodic nutrient input and periodic washout rate, respectively. The persistence inequality (5.1) is not always true for the two periodic models (3.1) and (4.1), hence we cannot get persistence. However, it is shown that in both cases, there are positive periodic solutions in the three dimensional spaces bifurcating from stable periodic solutions in the $N - P$ plane with the death rate of zooplankton used as the bifurcating parameter. Therefore, as in (5.1), if the death rate of zooplankton is relatively low, coexistence of all three components could occur.

The discrete delay due to ingestion and the distributed delay in the nutrient recycling can be introduced to the above zooplankton-phytoplankton-nutrient models. We will study this in Chapter 5.

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CHAPTER 3

A THREE-TROPHIC-LEVEL MODEL

3.1 Introduction

To date several attempts to model nutrient plankton dynamics have been made. Early models tended to concentrate on the interaction of phytoplankton and zooplankton only. More recently, models have become more holistic by attempting to embrace a larger portion of our knowledge of the components of the ecosystem and the flow of materials between these components. Williams [41] provided the conceptual background for a plankton dynamics model incorporating background for a plankton dynamics model incorporating bacteria, protozoans and dissolved organic matter. Evans and Parslow [13] presented a model of phytoplankton-zooplankton-nitrogen dynamics in a seasonably varying mixed layer. They showed how the seasonal recurrence of plankton cycles, in particular the spring bloom, is driven by the interaction of physical mixing with removal by grazers. DeAngelis, Bartell and Brenkect [9] studied the effects of nutrient recycling and food-chain length on resilience of a plankton model consisting of carnivore, herbivore, autotroph, detritus and nutrient. Fasham, Ducklow and McKelvie [14] constructed a simple but realistic model of plankton and nutrient dynamics of the oceanic mixed layer that includes the major plankton groups (plankton, zooplankton, bacteria) and the major forms of nitrogen (new and recycled inorganic forms, dissolved and particular organic forms).

An ecological system is virtually never totally closed to material fluxes from the outside; these are generally inputs of nutrients to the system, as well as losses from the system. Recently, Wroblewski, Sarmiento and Flierl [44] introduced a closed two-trophic-level food chain model which they used to study plankton densities in different ocean layers. Busenberg et al. [1] studied the stability of the model constructed by Wroblewski et al., and pursued the biological implications of the stability results and of the existence of stable oscillatory states. In [35], based on the model built by Wroblewski et al., we considered three open models consisting of phytoplankton, zooplankton and dissolved limiting nutrient with a constant input concentration of the limiting nutrient and different constant washout rates, a periodic input concentration and a constant washout rate, a constant input concentration and a periodic washout rate, respectively. Persistence and bifurcation were discussed.

In the present chapter, we consider a three-trophic-level food chain model with instantaneous nutrient recycling, which consists of autotrophic phytoplankton, herbivorous zooplankton, carnivorous zooplankton and dissolved limiting nutrient. We suppose that the carnivorous zooplankton (Z_2) feeds on the herbivorous zooplankton (Z_1), in turn the herbivorous zooplankton feeds upon the autotrophic phytoplankton (P), and only phytoplankton takes nutrient (N) directly. All dead carnivorous zooplankton, herbivorous zooplankton and phytoplankton are assumed to be recycled back into nutrient. We will consider the question of extinction and persistence of the three trophic level model. It is also shown that coexistence of all components may occur in the form of bifurcating periodic solutions. Similar three-trophic-level chemostat type models have been studied by Butler, Hsu and Waltman [3], Keener [26], (see also Butler and Wolkowicz [6], Wolkowicz [43] and Waltman [40]).

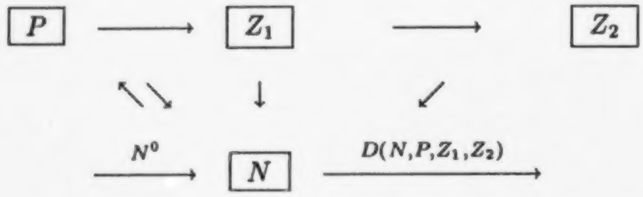

Fig. IV A three trophic level food chain for plankton dynamics with limit nutrient recycling. N^0 is the input rate of nutrient, DN is the washout rate of nutrient.

In our discussion, persistence is a central concept. We utilize the definitions of persistence developed by Butler, Freedman and Waltman [2] and Freedman and Moson [16]. A component $x(t)$ of a given system of ordinary differential equations is said to be *persistent* if for any $x(0) > 0$ it follows that $x(t) > 0$, $t > 0$ and $\liminf_{t\to\infty} x(t) > 0$. If there exists $\delta > 0$ (independent of $x(t)$) such that $x(t)$ is persistent and $\liminf_{t\to\infty} x(t) > \delta$, then $x(t)$ is said to be *uniformly persistent*. A system is (uniformly) persistent if each component is (uniformly) persistent. Persistence in biological systems has been discussed by many authors. We refer in particular to persistence in the four-dimensional models, (see Butler and Wolkowicz [6], So and Freedman [37], Freedman, So and Waltman [19], Freedman and Rai [17], Kumar and Freedman [31], Kirlinger [27], Takeuchi [39] and Zaghrout [45]). For the existence of periodic solutions in the four-dimensional models, we refer to Butler, Hsu and Waltman [3], Keener [26], and Freedman, So and Waltman [19].

The chapter is organized as follows. In the next section, we describe the model. In Section 3, we study questions of extinction and persistence. In Section 4 the bifurcation analysis is carried out. A discussion is in the final section.

3.2 The Model

The general abstract compartmental model used to describe a three-trophic-level food chain model consisting of autotrophic phytoplankton (P), herbivorous zooplankton (Z_1), carnivorous zooplankton (Z_2) and dissolved limiting nutrient (N), is given by the following system

$$\begin{aligned}
\frac{dN}{dt} &= D(N^0 - N) - aP\,\frac{N}{k+N} + (1-\delta)cZ_1(1-e^{-\lambda P}) \\
&\qquad + (1-\sigma)bZ_2\,\frac{Z_1^2}{\ell + Z_1^2} + \gamma P + \varepsilon Z_1 + \mu Z_2 \\
\frac{dP}{dt} &= aP\,\frac{N}{k+N} - cZ_1(1-e^{-\lambda P}) - (\gamma + D)P \\
\frac{dZ_1}{dt} &= Z_1[\delta c(1-e^{-\lambda P}) - (\varepsilon + D)] - bZ_2\,\frac{Z_1^2}{\ell + Z_1^2} \\
\frac{dZ_2}{dt} &= Z_2[\sigma b\,\frac{Z_1^2}{\ell + Z_1^2} - (\mu + D)], \\
N(0) \geq 0, &\quad P(0) > 0, \quad Z_1(0) > 0, \quad Z_2(0) > 0,
\end{aligned} \tag{2.1}$$

where all parameters are positive and are interpreted as follows.

N^0	is the input nutrient concentration rate
D	is the washout rate
a	is the maximal growth rate of the autotrophic phytoplankton
k	is the (Michaelis-Menten) half saturation constant
δ	is the herbivorous zooplankton resource conversion rate
σ	is the carnivorous zooplankton resource conversion rate
c	is the maximal herbivorous zooplankton ingestion rate
b	is the maximal carnivorous zooplankton ingestion rate
λ	is the rate at which saturation is achieved with decreasing phytoplankton

level

ℓ is the (Holling Type III) half saturation constant

γ is the phytoplankton death rate

ε is the herbivorous death rate

μ is the carnivorous death rate

We specify a constant input rate of dissolved limiting nutrient N^0 to the model, as well as a loss rate D. The uptake kinetics of the limiting nutrient is described by the Michaelis-Menten function or Holling Type II functional response (see Holling [23])

$$\frac{N}{k+N},$$

where k is a Michaelis-Menten half-saturation constant. This hyperbolic uptake rate was proposed by Dugdale [11] and has been widely employed (see Busenberg et al [1], Hallam [22] and Wroblewski et al [44]). Various laboratory and field experiments indicate this hyperbolic uptake response to nitrate, ammonium and phophate is reasonably appropriate (c.f. Rogers and McCarthy [34] and the references cited therein).

Marine copepods show an increasing ingestion rate as food concentrations increase. The functional form of this response has generally been of the Michaelis-Menten or Holling Type II shape showing a saturation of the ingestion rate with high prey concentrations. Commonly, Ivlev's functional response formulation (see Ivlev [24])

$$1-e^{-\lambda P}$$

is used to describe the herbivorous zooplankton grazing in curving-fitting and modelling (see Wroblewski et al [44]), where λ is the rate at which saturation is achieved with increasing phytoplankton level (per unit concentration).

The carnivorous zooplankton consumption of herbivorous zooplankton is modeled as Holling type III functional response (see Holling [23] and DeAngelis et al [9])

$$\frac{Z_1^2}{\ell + Z_1^2},$$

where ℓ is a Holling type III half-saturation constant. The representation is appropriate for situations in which the rate of predation per capita prey tends to become smaller as the biomass of prey decreases, which may often occur if there are refuges that give some of the prey protection from predators.

During consumption, only fractions of phytoplankton and herbivorous zooplankton removed from the resources compartments, δ $(\delta \leq 1)$ and $\sigma(\sigma \leq 1)$, are assumed to be assimilated by the consumers herbivore and carnivore respectively, the remains go directly to the dissolved limiting nutrient. Two other losses of biotic components are also modeled: (1) direct losses from autotrophic phytoplankton, herbivorous zooplankton and carnivorous zooplankton with loss rates γ, ε and μ respectively, to the dissolved limiting nutrient; and (2) removal of biotic components from the system (DP, DZ_1, and DZ_2) resulting from washout, harvesting or burial in deep sediments, for example.

Note that $E_1 = (N^0, 0, 0, 0)$ is always an equilibrium for system (2.1).

3.3 Extinction and Persistence

In this section, firstly we change the variables in system (2.1) to nondimensional ones. Let

$$\begin{aligned}
&\overline{N} = \frac{N}{N^0}\,, \quad \overline{P} = \frac{P}{N^0}\,, \quad \overline{Z}_1 = \frac{Z_1}{N^0}\,, \quad \overline{Z}_2 = \frac{Z_2}{N^0}\,, \\
&\overline{k} = \frac{k}{N^0}\,, \quad \overline{\ell} = \frac{\ell}{N^0}\,, \quad \overline{a} = \frac{a}{D}\,, \quad \overline{c} = \frac{c}{D}\,, \\
&\overline{b} = \frac{b}{D}\,, \quad \overline{\gamma} = \frac{\gamma}{D}\,, \quad \overline{\varepsilon} = \frac{\varepsilon}{D}\,, \quad \overline{\mu} = \frac{\mu}{D}\,, \\
&\qquad \bar{t} = Dt, \qquad \overline{\gamma} = \lambda N^0.
\end{aligned}$$

After dropping the bars, system (2.1) becomes

$$\begin{aligned}
\frac{dN}{dt} &= 1 - N - aP\,\frac{N}{k+N} + (1-\delta)cZ_1(1-e^{-\lambda P}) \\
&\quad + (1-\sigma)bZ_2\,\frac{Z_1^2}{\ell + Z_1^2} + \gamma P + \varepsilon Z_1 + \mu Z_2 \\
\frac{dP}{dt} &= aP\,\frac{N}{k+N} - cZ_1(1-e^{-\lambda P}) - (\gamma+1)P \\
\frac{dZ_1}{dt} &= Z_1[\delta c(1-e^{-\lambda P}) - (\varepsilon+1)] - bZ_2\,\frac{Z_1^2}{\ell+Z_1^2} \\
\frac{dZ_2}{dt} &= Z_2\big[\sigma b\,\frac{Z_1^2}{\ell+Z_1^2} - (\mu+1)\big] \\
N(0) &\geq 0, \quad P(0) > 0, \quad Z_1(0) > 0, \quad Z_2(0) > 0.
\end{aligned} \tag{3.1}$$

Note that for system (3.1), the equilibrium E_1 takes the form $E_1 = (1,0,0,0)$.

Lemma 3.1. *The omega limit set of any solution of the initial value problem (3.1) lies in the hyperplane* $N + P + Z_1 + Z_2 = 1$.

PROOF: Let $\Sigma(t) = N(t) + P(t) + Z_1(t) + Z_2(t)$, then

$$\frac{d\Sigma(t)}{dt} = 1 - \Sigma(t), \quad \Sigma(0) \geq 0,$$

and the lemma follows. □

We can use Lemma 3.1 to eliminate one variable from system (3.1), then the four dimensional system (3.1) can be changed to a three dimensional one:

$$\begin{aligned}\frac{dP}{dt} &= aP\left[\frac{a(1-P-Z_1-Z_2)}{1+k-P-Z_1-Z_2}-(\gamma+1)\right]-cZ_1(1-e^{-\lambda P})\\ \frac{dZ_1}{dt} &= Z_1[\delta c(1-e^{-\lambda P})-(\varepsilon+1)]-bZ_2\,\frac{Z_1^2}{\ell+Z_1^2} \qquad (3.2)\\ \frac{dZ_2}{dt} &= Z_2\left[\sigma b\,\frac{Z_1^2}{\ell+Z_1^2}-(\mu+1)\right].\end{aligned}$$

Since every trajectory is asymptotic to its omega limit set, it is sufficient to analyze system (3.2). Note that the positive cone in (N, P, Z_1, Z_2)-plane is positively invariant under the solution map, Lemma 3.1 implies the boundedness of solutions of systems (3.1). Also by Lemma 3.1, trajectories which form the positive omega limit set of any solution of (3.1) are solutions of (3.2) satisfying $0 \le P, Z_1, Z_2 \le 1$.

Denote

$$\theta_1 = \frac{k}{\frac{a}{\gamma+1}-1}, \quad \theta_2 = \frac{e^{-\lambda}}{1-\frac{\varepsilon+1}{\delta c}}, \quad \theta_3 = \frac{\ell}{\frac{\sigma b}{\mu+1}-1}.$$

In the following we give criteria for autotrophic phytoplankton or herbivorous zooplankton or carnivorous zooplankton or all of them to become extinct.

Theorem 3.2. *If one of the following ineqalities*

$$\sigma b \le \mu+1 \quad \text{or} \quad \theta_3 \ge 1, \qquad (3.3)$$

hold but not both, then $\lim_{t\to\infty} Z_2(t) = 0$.

PROOF: From the fourth equation of system (3.1), we have that

$$\begin{aligned}\frac{dZ_2}{dt} &= Z_2\left[\sigma b\,\frac{Z_1^2}{\ell + Z_1^2} - (\mu+1)\right] \\ &= Z_2\,\frac{\sigma b - (\mu+1)}{\ell + Z_1^2}\left[Z_1^2 - \frac{\ell(\mu+1)}{\sigma b - (\mu+1)}\right] \\ &\leq Z_2\,\frac{\sigma b - (\mu+1)}{\ell + Z_1^2}\,(1-\theta_3) \\ &\leq 0 \quad \text{(by (3.3))}.\end{aligned}$$

Since there are no invariant sets such that $Z_2 > 0$ is constant, the theorem follows. □

This theorem indicates that if the growth rate of the carnivorous zooplankton is less than or equal to its loss rate, or if the parameter θ_3 is greater than or equal to one, than the carnivorous zooplankton population will die out.

Theorem 3.3. *If one of the following inequalities*

$$\delta c \leq \varepsilon + 1 \quad \text{or} \quad \theta_2 \geq 1, \tag{3.4}$$

holds but not both, then $\lim_{t\to\infty} Z_1(t) = 0$ *and consequently* $\lim_{t\to\infty} Z_2(t) = 0$.

PROOF: By the third equation of (3.1) we have

$$\begin{aligned}\frac{dZ_1}{dt} &< Z_1[\delta c(1-e^{-\lambda P}) - (\varepsilon+1)] \\ &= Z_1[\delta c - (\varepsilon+1)]\left[1 - \frac{\delta c e^{-\lambda P}}{\delta c - (\varepsilon+1)}\right] \\ &\leq Z_1[\delta c - (\varepsilon+1)](1-\theta_2)\end{aligned}$$

$$\leq 0 \quad \text{(by (3.4))}.$$

Since there are no invariant sets such that $Z_1 > 0$ is constant, $Z_1(t) \to 0$ as $t \to \infty$. Also, carnivorous zooplankton depends on herbivorous zooplankton for its survival, so $Z_1(t) \to 0$ implies $Z_2(t) \to 0$ as $t \to \infty$. Hence the theorem follows. □

Similarly, Theorem 3.3 shows that if the growth rate of the herbivorous zooplankton is less than or equal to its loss rate (death rate plus washout rate), or the parameter θ_2 is greater than or equal to one, than the herbivorous zooplankton population, and hence the carnivorous zooplankton population will become extint.

Theorem 3.4. *If one of the following inequalities*

$$a \leq \gamma + 1 \quad \text{or} \quad \theta_1 \geq 1, \tag{3.5}$$

holds but not both, then $\lim_{t\to\infty} P(t) = 0$ *and consequently* $\lim_{t\to\infty} Z_1(t) = \lim_{t\to\infty} Z_2(t) = 0$.

PROOF: Similar to the proof of Theorem 3.3, we have

$$\begin{aligned} \frac{dP}{dt} &< P\left[\frac{aN}{k+N} - (\gamma+1)\right] \\ &\leq P\left[\frac{a}{1+k} - (\gamma+1)\right] \\ &= P\,\frac{a-(\gamma+1)}{1+k}\left[1 - \frac{k(\gamma+1)}{a-(\gamma+1)}\right] \\ &= P\,\frac{a-(\gamma+1)}{1+k}(1-\theta_1) \\ &\leq 0 \quad \text{(by (3.5))}, \end{aligned}$$

which completes the proof. □

This result demonstrates that if the maximum growth rate of phytoplankton is less than or equal to its loss rate, or the parameter θ_1 is greater than or equal to one, then all the planktons will become extinct.

From Theorem 3.2, 3.3 and 3.4 we have the following

Theorem 3.5. *If one of the inequalities in (3.5) holds, then*

$$\lim_{t\to\infty} \big(N(t), P(t), Z_1(t), Z_2(t)\big) = E_1.$$

If any of the inequalities (3.3), (3.4) and (3.5) holds, persistence can not occur in system (3.1). From now on, we always assume that the inverse direction inequalities of (3.3), (3.4) and (3.5) hold, i.e.

(A_1) $a > \gamma + 1$ and $\theta_1 < 1$.

(A_2) $\delta c > \varepsilon + 1$ and $\theta_2 < 1$.

(A_3) $\sigma b > \mu + 1$ and $\theta_3 < 1$.

Denote

$$\begin{aligned} H_1 &= \{(N, P, Z_1, Z_2) \in R^4_+ \mid P = Z_1 = Z_2 = 0\}, \\ H_{12} &= \{(N, P, Z_1, Z_2) \in R^4_+ \mid Z_1 = Z_2 = 0\}, \\ H_{123} &= \{(N, P, Z_1, Z_2) \in R^4_+ \mid Z_2 = 0\}. \end{aligned}$$

Clearly $E_1 = (1, 0, 0, 0)$ is globally asymptotically stable in Int H_1, which denotes the interior of H_1, and E_1 is hyperbolic if (see Freedman and So [18],

p. 80)

$$\frac{1}{k+1} > \frac{\gamma+1}{a}\,. \tag{3.6}$$

If the autotrophic phytoplankton is at the top trophic level, we have the subsystem

$$\begin{aligned} \frac{dN}{dt} &= 1 - N - aP\,\frac{N}{k+N} + \gamma P \\ \frac{dP}{dt} &= P\big[a\,\frac{N}{k+N} - (\gamma+1)\big]. \end{aligned} \tag{3.7}$$

System (3.7) has an interior equilibrium $(\overline{N}, \overline{P})$, where

$$\overline{N} = \frac{k(\gamma+1)}{a-(\gamma+1)}\,, \qquad \overline{P} = \frac{a-(k+1)(\gamma+1)}{a-(\gamma+1)}$$

provided $a > \gamma + 1$. Choosing a Liapunov function $V_1(N,P)$ as follows

$$V_1(N,P) = \int_{\overline{N}}^{N} \frac{\frac{x}{k+x} - \frac{\gamma+1}{a}}{\frac{x}{k+x}}\,dx + \frac{1}{\gamma+1}\int_{\overline{P}}^{P} \frac{y-\overline{P}}{y}\,dy,$$

it is not difficult to prove that $(\overline{N}, \overline{P})$ is globally asymptotically stable in the $N - P$ plane (see Ruan [33]), that is, system (3.1) has an equilibrium $E_2 = (\overline{N}, \overline{P}, 0, 0)$ which is globally asymptotically stable with respect to Int H_{12}, and E_2 is hyperbolic if

$$1 - e^{-\lambda \overline{P}} > \frac{\varepsilon+1}{\delta c}\,. \tag{3.8}$$

If the herbivorous zooplankton Z_1 is at the highest trophic level, we have the following subsystem

$$\begin{aligned} \frac{dN}{dt} &= 1 - N - aP\,\frac{N}{k+N} + (1-\delta)cZ_1(1-e^{-\lambda P}) + \gamma P + \varepsilon Z_1 \\ \frac{dP}{dt} &= aP\,\frac{N}{k+N} - cZ_1(1-e^{-\lambda P}) - (\gamma+1)P \\ \frac{dZ_1}{dt} &= Z_1[\delta c(1-e^{-\lambda P}) - (\varepsilon+1)]. \end{aligned} \tag{3.9}$$

System (3.9) has an interior equilibrium $(\widetilde{N}, \widetilde{P}, \widetilde{Z}_1)$ if $\delta c > \varepsilon + 1$, where

$$\widetilde{P} = \frac{1}{\lambda} \ln \frac{\delta c}{\delta c - (\varepsilon+1)},$$

$\widetilde{Z}_1$ is the positive solution, satisfies $\widetilde{Z} < 1 - \widetilde{P}$, of the quadratic equation

$$\begin{aligned} Z_1^2 - \Big[\Big(\frac{\delta(a-\gamma-1)}{\varepsilon+1} - 1\Big)\widetilde{P} + k + 1\Big] Z_1 & \\ + \widetilde{P}\,\frac{\delta}{\varepsilon+1}\,[(a-\gamma-1)(1-\widetilde{P}) - k(\gamma+1)] &= 0, \end{aligned} \tag{3.10}$$

and

$$\widetilde{N} = 1 - \widetilde{P} - \widetilde{Z}_1.$$

Hence system (3.1) has an equilibrium $E_3 = (\widetilde{N}, \widetilde{P}, \widetilde{Z}_1, 0)$. Define a Liapunov function

$$V_2(N,P,Z_1) = \int_{\widetilde{N}}^{N} \frac{x - \widetilde{N}}{x} dx + \int_{\widetilde{P}}^{P} \frac{\delta c(1-e^{-\lambda y}) - (\varepsilon+1)}{1-e^{-\lambda y}} dy + \int_{\widetilde{Z}_1}^{Z_1} \frac{z - \widetilde{Z}_1}{z} dz.$$

The derivative of V along trajectories of (3.9) is

$$\frac{dV_2}{dt} = \frac{N-\widetilde{N}}{N}\Big(1 - N - aP\frac{N}{k+N} + (1+\delta)cZ_1(1-e^{-\lambda P}) + \gamma P + \varepsilon Z_1\Big)$$

$$+ [\delta c(1-e^{-\lambda P}) - (\varepsilon+1)]\Big\{\frac{P}{1-e^{-\lambda P}}[a\frac{\widetilde{N}}{k+\widetilde{N}} - (\gamma+1)] - c\widetilde{Z}_1\Big\}$$

$$+ \frac{aP}{1-e^{-\lambda P}}[\delta c(1-e^{-\lambda P}) - (\varepsilon+1)]\left[\frac{N}{k+N} - \frac{\widetilde{N}}{k+\widetilde{N}}\right].$$

Define $\phi_1(N), \phi_2(P)$ and $\psi_2(P)$ as follows

$$\phi_1(N) = \frac{k}{(k+\xi_1 N)^2}, \quad 0 < \xi_1 < 1,$$

$$\phi_2(P) = \lambda e^{-\lambda\xi_2 P}, \quad 0 < \xi_2 < 1,$$

$$\psi_2(P) = -\left[\frac{a\widetilde{N}}{k+\widetilde{N}} - (\gamma+1)\right]\frac{(1+\lambda\xi_3 P)e^{-\lambda\xi_3 P} - 1}{(1-e^{-\lambda\xi_3 P})^2}, \quad 0 < \xi_3 < 1,$$

such that

$$\frac{N}{k+N} - \frac{\widetilde{N}}{k+\widetilde{N}} = \phi_1(N)(N-\widetilde{N}),$$

$$\delta c(1-e^{-\lambda P}) - (\varepsilon+1) = \delta c\phi_2(P)(P-\widetilde{P}),$$

$$\frac{P}{1-e^{-\lambda P}}\left[\frac{a\widetilde{N}}{k+\widetilde{N}} - (\gamma+1)\right] - c\widetilde{Z}_1 = \psi_2(P)(P-\widetilde{P}).$$

Then

$$\frac{dV_2}{dt} = -\frac{1}{N}(1 + a\widetilde{P}\phi_1(N))(N-\widetilde{N})^2$$

$$+ \left[\frac{\gamma}{N} + (1-\delta)c\widetilde{Z}_1\frac{\phi_2(P)}{N} + a\delta c\phi_1(N)\frac{P\phi_2(P)}{1-e^{-\lambda P}} - \frac{a}{k+N}\right](N-\widetilde{N})(P-\widetilde{P})$$

$$+ \frac{1}{N}[\varepsilon + (1-\delta)c(1-e^{-\lambda\widetilde{P}})](N-\widetilde{N})(Z_1-\widetilde{Z}_1)$$

$$
\begin{aligned}
&- \delta c\phi_2(P)\psi_2(P)(P-\widetilde{P})^2 \\
&+ (1-\delta)c\frac{N-\widetilde{N}}{N}\phi_2(P)(P-\widetilde{P})(Z_1-\widetilde{Z}_1) \\
= {}& WSW^T,
\end{aligned}
$$

where $W = (N-\widetilde{N}, P-\widetilde{P}, Z_1-\widetilde{Z}_1)$ and the function matrix $S = (s_{ij})_{3\times 3}$ is defined as

$$
\begin{aligned}
s_{11} &= -\frac{1}{N}(1 + a\widetilde{P}\phi_1(N)), \\
s_{22} &= -\delta c\phi_2(P)\psi_2(P), \\
s_{33} &= 0, \\
s_{12} = s_{21} &= \frac{1}{2}\left[\frac{\gamma}{N} + (1-\delta)c\widetilde{Z}_1\frac{\phi_2(P)}{N} + a\delta c\phi_1(N)\frac{P\phi_2(P)}{1-e^{-\lambda P}} - \frac{a}{k+N}\right], \\
s_{13} = s_{31} &= \frac{1}{2N}[\varepsilon + (1-\delta)c(1-e^{-\lambda\widetilde{P}})], \\
s_{23} = s_{32} &= \frac{1}{2}(1-\delta)c\frac{N-\widetilde{N}}{N}\phi_2(P).
\end{aligned}
$$

If S is negative definite for all $(N, P, Z_1) \in H_{123}$, then E_3 is globally asymptotically stable with respect to H_{123} (c.f. Freedman and So [18]). Now we can make the following assumption

(A_4) The equilibrium $E_3 = (\widetilde{N}, \widetilde{P}, \widetilde{Z}_1, 0)$ is globally asymptotically stable with respect to H_{123}.

Similarly, if the inequality

$$\frac{\widetilde{Z}_1^2}{\ell + \widetilde{Z}_1^2} > \frac{\mu+1}{\sigma b} \tag{3.11}$$

holds, E_3 is hyperbolic.

Remark: Inequalities (3.6), (3.8) and (3.11) imply the inequalities $a > \gamma + 1$, $\delta c > \varepsilon + 1$ and $\sigma b > \mu + 1$, respectively.

Theorem 3.6. *Suppose that assumptions $(A_1) - (A_4)$ and inequalities (3.6), (3.8) and (3.11) hold. Then system (3.1) exhibits uniform persistence.*

PROOF: By Lemma 3.1, system (3.1) is dissipative. Now $\mathcal{M} = \{E_1, E_2, E_3\}$ is the isolated covering. Inequality (3.6) implies that E_1 is hyperbolic, so E_1 is a saddle point. Since E_1 is globally asymptotically stable with respect to H_1, it follows that $H_1 \subset W^+(E_1)$ (the stable set of E_1), hence $W^+(E_1) \cap R^4_+ = \emptyset$.

E_2 is also a saddle point and is globally asymptotically stable with respect to H_{12}, and it has a one-dimensional unstable manifold whose direction is out of the plane H_{12}, hence $W^+(E_2) \cap R^4_+ = \emptyset$. Similar statements apply to E_3.

The global asymptotic stability of E_1, E_2 and E_3 with respect to H_1, H_{12} and H_{123} respectively also implies that the boundary flow is isolated and acyclic with $\mathcal{M}$. Therefore, by Theorem 3.1 of Butler and Waltman [5], uniform persistence follows. $\square$

Theorem 3.6 shows that if near the boundary equilibria E_1, E_2 and E_3, the growth rates of phytoplankton, herbivorous zooplankton and carnivorous zooplankton are positive, respectively, and all the parameters θ_1, θ_2 and θ_3 are less than one, then all components have long term survival.

By Theorem 5 of Hutson [24], we have the following result.

Theorem 3.7. *Under the hypothesis of Theorem 3.6, the system (3.1) has an interior equilibrium $E^* = (N^*, P^*, Z_1^*, Z_2^*)$.*

3.4. Coexistence

Now we consider subsystem (3.9), the special case $Z_2 \equiv 0$ in (3.1). After dropping subscripts we have

$$\begin{aligned}
\frac{dN}{dt} &= 1 - N - ap\,\frac{N}{k+N} + (1-\delta)cZ(1-e^{-\lambda p}) + \gamma P + \varepsilon Z \\
\frac{dP}{dt} &= aP\,\frac{N}{k+N} - cZ(1-e^{-\lambda P}) - (\gamma+1)P \\
\frac{dZ}{dt} &= Z[\delta c(1-e^{-\lambda P}) - (\varepsilon+1)],
\end{aligned} \tag{4.1}$$

$$N(0) \geq 0, \quad P(0) > 0, \quad Z(0) > 0.$$

System (4.1) inherits from the larger system (3.1) the properties that the positive octant is positively invariant, that $a \leq \gamma + 1$ or $\theta_1 \geq 1$ forces $\lim_{t\to\infty} P(t) = 0$ (and hence $\lim_{t\to\infty} Z(t) = 0$) that $\delta c \leq \varepsilon + 1$ or $\theta_2 \leq 1$ forces $\lim_{t\to\infty} Z(t) = 0$, and that the omega limit set of any solution of (4.1) lies in the set

$$\Delta_1 = \{(N,P,Z) | N + P + Z = 1, \quad N \geq 0, \quad P \geq 0, \quad Z \geq 0\}.$$

Since every trajectory is asymptotic to its omega limit set, it suffices to analyze the system

$$\begin{aligned}
\frac{dP}{dt} &= P\left[\frac{a(1-P-Z)}{1+k-P-Z} - (\gamma+1)\right] - cZ(1-e^{-\lambda P}) \\
\frac{dZ}{dt} &= Z[\delta c(1-e^{-\lambda P}) - (\varepsilon+1)].
\end{aligned} \tag{4.2}$$

Note that we may restrict our attention to the triangular region

$$\Delta_2 = \{(P,Z) | 0 \leq P,\ Z,\ P + Z \leq 1\}.$$

The critical points on the boundary of Δ_1 for (4.2) are

$$C_1 = (0,0), \quad C_2 = (1 - \theta_1, 0).$$

The variational matrix of (4.2) takes the form

$$M = \begin{pmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{pmatrix},$$

where

$$m_{11} = \frac{a(1-P-Z)}{1+k-P-Z} - \frac{akP}{(1+k-P-Z)^2} - (\gamma+1) - c\lambda Z e^{-\lambda P},$$

$$m_{12} = -\frac{akP}{(1+k-P-Z)^2} - c(1 - e^{-\lambda P}),$$

$$m_{21} = \delta c \lambda Z e^{-\lambda P},$$

$$m_{22} = \delta c(1 - e^{-\lambda P}) - (\varepsilon + 1).$$

At $C_1 = (0,0)$, the variational matrix has the form

$$M_1 = \begin{pmatrix} \dfrac{[a-(\gamma+1)](1-\theta_1)}{1+k} & 0 \\ 0 & -(\varepsilon+1) \end{pmatrix}.$$

Thus, if $a < \gamma + 1$ or $\theta_1 > 1$, C_1 is an asymptotically stable critical point, and if $a > \gamma + 1$ and $\theta_1 < 1$ (which we are assuming), then C_1 is a saddle point.

At $C_2 = (1-\theta_1, 0)$, M takes the form

$$M_2 = \begin{pmatrix} -\dfrac{ak(1-\theta_1)}{(k+\theta_1)^2} & -\dfrac{ak(1-\theta_1)}{(k+\theta_1)^2} - c(1 - e^{-\lambda(1-\theta_1)}) \\ 0 & [\delta c - (\varepsilon+1)](1 - \theta_2 e^{\lambda\theta_1}) \end{pmatrix}.$$

For C_2 to be biologically meaningful, i.e., to be in the positive quadrant, it must be the case that $0 < \theta_1 < 1$. So if $\theta_2 e^{\lambda\theta_1} > 1$, C_2 is an asymptotically stable critical point, if $0 < \theta_2 e^{\lambda\theta_1} < 1$, C_2 is a saddle point.

Let (P_c, Z_c) be a critical point in the interior of Δ_2, i.e.

$$P_c\left[\frac{a(1-P_c-Z_c)}{1+k-P_c-Z_c}-(\gamma+1)\right]-cZ_c(1-e^{-\lambda P_c})=0, \tag{4.3}$$

$$\delta c(1-e^{-\lambda P})-(\varepsilon+1)=0. \tag{4.4}$$

From (4.4) we have that

$$P_c = 1-\frac{1}{\lambda}\ln\frac{1}{\theta_2} \quad (\text{if} \quad \theta_2 < 1), \tag{4.5}$$

so we are assuming that $Z_c > 0$ satisfies (4.3) and it may be rewritten as the following

$$\lambda\delta k(\gamma+1)\left(\frac{1}{\lambda}\ln\frac{1}{\theta_2}-\theta_1-Z_c\right)=\left[(\lambda k-a)Z_c-\frac{a}{\lambda}\ln\frac{1}{\theta_2}\right](\varepsilon+1)\theta_1.$$

If $\theta_1 > \frac{1}{\lambda}\ln\frac{1}{\theta_2}$, i.e. $\theta_2 e^{\lambda\theta_1} > 1$, (4.3) has no positive solution. Thus if C_2 is asymptotically stable, there is no interior critical point. If $\theta_2 e^{\lambda\theta_1} < 1$, then (4.3) has precisely one positive solution Z_c.

The variational matrix at (P_c, Z_c) has the form

$$M_3 = \begin{pmatrix} \dfrac{Z_c[(\varepsilon+1)\theta_2 e^{\lambda}-c\lambda\delta+c\delta\ln\frac{1}{\theta_2}]}{\theta_2\delta e^{\lambda}(1-\frac{1}{\lambda}\ln\frac{1}{\theta_2})}-\dfrac{ak(1-\frac{1}{\lambda}\ln\frac{1}{\theta_2})}{(k+\frac{1}{\lambda}\ln\frac{1}{\theta_2}-Z_c)^2} & -\dfrac{ak(1-\frac{1}{\lambda}\ln\frac{1}{\theta_2})}{(k+\frac{1}{\lambda}\ln\frac{1}{\theta_2}-Z_c)^2}-\dfrac{\varepsilon}{\quad} \\ \dfrac{\delta c\lambda Z_c}{\theta_2 e^{\lambda}} & 0 \end{pmatrix}$$

If $\theta_2 > e^{-\lambda}$, i.e. $1-\frac{1}{\lambda}\ln\frac{1}{\theta_2} > 0$, the determinant of M_3 is positive, then the stability of (P_c, Z_c) depends upon the trace of M_3, i.e., if

$$\frac{Z_c[(\varepsilon+1)\theta_2 e^{\lambda} - c\lambda\delta + c\delta \ln \frac{1}{\theta_2}]}{\theta_2 \delta e^{\lambda}(1 - \frac{1}{\lambda}\ln\frac{1}{\theta_2})^2} < \frac{ak}{(k + \frac{1}{\lambda}\ln\frac{1}{\theta_2} - Z_c)^2}\,, \tag{4.6}$$

(P_c, Z_c) is asymptotically stable.

System (4.2) is different from the Gause-type predator-prey systems described by Kuang and Freedman [30], and the chemostat type systems investigated by Cheng [6], Liou and Cheng [32], Ding [10] and Kuang [28]. The uniqueness theorems about the limit cycle and the methods utilized there do not seem to work for system (4.2). However, by a result of Erle [12], we know that system (4.2) has at most a finite number of limit cycles and if (P_c, Z_c) is unstable, (4.2) must have at least one asymptotically stable limit cycle. We make the following assumption (see Butler, Hsu and Waltman [3] and Freedman, So and Waltman [19]).

(A_5) There exists a limit cycle for system (4.2) which has a Floquet multiplier strictly inside the unit circle.

Let $(P(t), Z_1(t))$ be a periodic solution of period τ of system (4.2) which is given by (A_5) for the parameters $a, k, \gamma, c, \lambda, \delta$ and ε. Then $(P(t), Z_1(t), 0)$ is a solution of system (3.2) for any choice of parameters b, σ, ℓ and μ. Now fix b, σ and μ and define

$$h(\ell) = \frac{\sigma b}{\tau}\int_0^{\tau} \frac{Z_1^2(\xi)}{\ell + Z_1^2(\xi)}\, d\xi,$$

where ℓ will be treated as a bifurcation parameter.

Let Γ be the orbit corresponding to the solution $(P(t), Z_1(t), 0)$. Let Ω be a two-dimensional local transverse section of Γ, let W_0 and W_1 be open subsets of Ω. For each value of ℓ, the Poincaré map $T : W_0 \to W_1$ exists. For a given periodic orbit, the linearization about the periodic orbit and the linearization of the Poincaré map about the fixed point corresponding to Γ are related, which is precisely made in the following statement (see Marsden and McCracken [33]).

Lemma 4.1. *The spectrum of the linearization of the Poincaré map union* $\{1\}$ *is equal to the spectrum of the linearization of the solution map defined by*

$$\Phi(P^0, Z_1^0, Z_2^0) = \big(P(\tau), Z_1(\tau), Z_2(\tau)\big),$$

where

$$P(0) = P^0, \quad Z_1(0) = Z_1^0, \quad Z_2(0) = Z_2^0$$

and τ *is the period of the periodic solution map.*

As a consequence, to show that one Floquet multiplier passes from inside to outside the unit circle is equivalent to show that an eigenvalue of the linearization of the Poincaré map passes from inside to the outside the unit circle. For this, we need the following bifurcation theorem in Marsden and McCraken [33] (see also [8]).

Lemma 4.2. *Let* W *be an open neighbourhood of* $0 \in R^2$ *and* I *be an open interval about* $0 \in R$. *Let* $\Phi_v : W \to R^n$ *be such that the map* $(v, x) \to \Phi_v(x)$ *is a* C^k *map* $(k \geq 1)$ *from* $I \times W$ *to* R^2, *and such that* $\Phi_v(0) = 0$ *for all* $v \in I$. *Define* L_v *to be the differential map* $d\Phi_v(0)$ *and suppose that all eigenvalues of* L_v *lie inside the unit circle of the complex plane for* $v < 0$. *Assume that there is a real, simple eigenvalue* $\ell(v)$ *of* L_v *such that* $\ell(0) = 1$ *and* $\frac{d\ell}{dv}(0) > 0$. *Let* v_0 *be the eigenvector corresponding to* $\ell(0)$. *Then there is a* C^{k-1} *curve* C *of fixed points of* $\Phi : (v, x) \to \big(v, \Phi_v(x)\big)$ *near* $(0,0)$ *in* $I \times R^2$ *which together* *with the points* $(v, 0)$ *are the only fixed points of* Φ *near* $(0,0)$. *The curve* C *is tangent to* v_0 *at* $(0,0)$ *in* $I \times R^2$.

The following theorem is the main result of this section.

Theorem 4.3. *Let* $a, k, \gamma, c, \lambda, \delta, \varepsilon, b, \sigma$ *and* μ *be fixed so that* (A_1), (A_2), *the first inequality of* (A_3), *and* (A_5) *hold. Then there exists a number* ℓ^* *such that for* $\ell < \ell^*$, $|\ell^* - \ell|$ *sufficiently small, system (3.1) has a periodic orbit in* R^4_+ *arbitrarily near the plane* $N + P + Z_1 = 1$, $Z_2 = 0$.

PROOF: The proof is heavily dependent upon the techniques used by Butler, Hsu and Waltman [3] and Freedman, So and Waltman [19]. Let $\left(P(t), Z_1(t)\right)$ be the unique periodic solution of (4.2), the Floquet expoents are 0 and $-\alpha < 0$. Let ℓ^* be an undetermined constant, and let $v = \ell^* - \ell$. Let Γ be the orbit associated with the periodic solution $\left(P(t), Z_1(t), 0\right)$ when $\ell = \ell^*$. Fix a point $x_0 \in \Gamma$ and let Ω be the transverse section to Γ at x_0, identifying x_0 with $0 \in R^2$. Let Φ_v be the Poincaré map associated with the periodic solution $\left(P(t), Z_1(t), 0\right)$ from v near 0. From the analytic dependence of the vector field defined by (4.2) on its parameters, it follows that the solutions are analytic in parameters and initial conditions, and so is the Poincaré map. Hence there is a neighborhood W_0 of x_0 in Ω such that for all v sufficiently close to zero, Φ_v is defined on W_0.

Now we study the spectrum of $L_v = d\Phi_v(0)$ by examining the Floquet multipliers of the corresponding system of differential equations. The variational matrix associated with the linearization of (3.2) takes the form

$$\begin{pmatrix} f_P(P(t),Z_1(t),0) & f_{Z_1}(P(t),Z_1(t),0) & f_{Z_2}(P(t),Z_1(t),0) \\ \delta c\lambda Z e^{-\lambda P(t)} & \delta c(1-e^{-\lambda P})-(\varepsilon+1) & -\dfrac{bZ_1^2}{\ell+Z_1^2} \\ 0 & 0 & \dfrac{\sigma b Z_1^2}{\ell+Z_1^2}-(\mu+1) \end{pmatrix},$$

where $\frac{dP}{dt}=f(P,Z_1,Z_2)$ in (3.2). The two-dimensional system

$$\frac{d}{dt}\begin{pmatrix} P(t) \\ Z_1(t) \end{pmatrix} = A(t)\begin{pmatrix} P(t) \\ Z_1(t) \end{pmatrix}$$

has one Floquet multiplier equal to 1 since $(P(t),Z_1(t))^T$ is a periodic solution and one multiplier inside the unit circle, call it $e^{-\alpha}$, by the hypothesis (A5). The third Floquet multipler of the full system has the form $\exp[h(\ell)-(\mu+1)]$.

Since $h(0)=\sigma b>(\mu+1)$ by assumption (A3) and

$$h(\ell)\le\frac{\sigma b}{\ell\tau}\int_0^\tau x^2(\zeta)\,d\zeta,$$

if ℓ is sufficiently large, $h(\ell)$ is arbitrarily small. Note that $h(\ell)$ is continuous and decreasing with ℓ, there is a unique value ℓ^* such that $h(\ell^*)=\mu+1$. Note also that

$$\frac{dh}{d\ell}=-\frac{\sigma b}{\tau}\int_0^\tau\frac{x^2(\zeta)}{(\ell+x^2(\zeta))^2}\,d\zeta<0,$$

in particular, when r passes through 0, i.e., ℓ passes through ℓ^*, $h(\ell)$ crosses the value $\mu+1$ non-tangentially, and

$$\frac{\partial e^r}{\partial\ell}(\ell^*)=\frac{dh}{d\ell}(\ell^*)\cdot e^{h(\ell^*)-(\mu+1)}<0$$

as $r = h(\ell) - (\mu + 1)$ passes through zero. Thus $\frac{\partial e^r}{\partial v}(0) > 0$ (where $v = \ell^* - \ell$), so the Floquet multiplier passes through the unit circle transversally.

We know that the Poincaré map is analytic in parameter and initial conditions, so $(v, x) \to \Phi_v(x)$ is analytic from $I \times W$, $\Phi_v(0) = 0$ for all $v \in I$ and $L_v = d\Phi_v(0)$ has eigenvalues $e^{-\alpha}$ and e^r, and crosses the unit circle non-tangentially as r passes through zero.

Applying Lemma 4.2, we obtain an C^1 curve $\mathcal{C}$ of fixed points of $\Phi :$ $(v, x) \to (v, \Phi_v(x))$ bifurcating from $(v, 0)$ at $(0, 0)$. For such (v, x), we have $x = \Phi_v(x)$, so x is a fixed point of the Poincaré map Φ_v, therefore $\mathcal{C}$ correspond to a 1-parameter family of periodic solutions of (4.1) hence (3.1). Since $\mathcal{C}$ is tangent to the eigenvector associated with the eigenvalue 1 of $L_v = d\Phi(0)$, the direction of v_0 is transverse to the P-Z_1 plane, so $\mathcal{C}$ is transverse to the P-Z_1 plane. It follows that there is a branch of periodic solutions of (3.1) in the positive octant if $|\ell - \ell^*| = |v|$ is sufficiently small. This completes the proof of the theorem. $\square$

3.5 Discussion

We have considered a three-trophic-level model of plankton dynamics with instantaneous nutrient recycling, which consisted of autotrophic phytoplankton, herbivorous zooplankton, carnivorous zooplankton and dissolved limiting nutrient. We suppose that there are a constant input concentration to the system, and a constant washout rate from the system.

Firstly we gave criteria for autotrophic phytoplankton or herbivorous zooplankton or carnivorous zooplankton or all of them to become extinct. The extinction results imply that bifurcation can occur. Since predator-prey system can have an oscillatory tendency, it is natural to seek oscillatory coexistence of all elements of the population. Next we have studied the questions of persistence, sufficient conditions are given which guarantee the survival of all elements of the population, which also imply the existence of a interior equilibrium in the positive cone.

Finally, under appropriate circumstance, a bifurcation theorem is used to show that coexistence of the autotroph, herbivore and carnivore occurs in the form of bifurcating periodic orbit.

It would be of great interest to investigate the homogeneous Neumann problem and Dirichelet problem for reaction-diffusion models of plankton nutrient dynamics, we propose to do this in Chapter 4.

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CHAPTER 4

REACTION-DIFFUSION MODELS

4.1 Introduction

In the oceans, plankton population movement is subject to many factors, e. g. currents and turbulent laterial diffusion. Hence the equations used to model the dynamics of plankton-nutrient interaction often take the form of nonlinear parabolic partial differential equations, or reaction-diffusion equations.

Kierstead and Slobodkin [12] proposed a simple linear scalar diffusion equation as a model for the study of plankton bloom which took the form of a logistic equation with a simple diffusion term added on to it. This is a special case of a more general scalar equation with a Laplace operator, which occurs not only in ecology, but also in physics, chemistry, general life sciences, etc. (see, [5], [20], [21], [28]).

Steele [30] reported that plankton displayed spatial heterogeneity in a homogeneous environment in spite of the diffusion process. In [31], Steele extended the basic notion of Kierstead and Slobodkin [12] and proposed several prey and predator systems with the addition of diffusion as models for the interaction between two kinds of plankton, i.e. phytoplankton (the prey) and herbivorous zooplankton (the predator), and suggested a mechanism for patch formation. Steele's model was based on Lotka-Volterra dynamics and was extended to more general dynamics by Mimura [19]. The more general predator-prey models were studied by Conway and Smoller [4], (see also [2], [9], [25]).

In [24], Radach and Maier-Reimer developed a three dimensional degenerate reaction-diffusion model consisting of phytoplankton, limiting nutrient and light intensity. The existence and uniqueness of solutions of this model were studied by

Wörz-Busekros [33] utilizing Picard's method.

Wroblewski [34] and Wroblewski and O'Brien [36] constructed several reaction-diffusion models to demonstrate how numerical modeling can clarify and help evaluate the complex biological and physical relations involved in oceanic sound scattering. Their models represented dissolved nutrient (N), phytoplankton (P) and herbivorous zooplankton (Z). The herbivore community was divided into two subpopulation ratios Z_1 and Z_2. Ratio Z_1 represented that portion of Z located in the surface waters where it could graze on the phytoplankton patch, whereas ratio Z_2 represented the remaining portion of Z which had vertically migrated downward to the point where it could no longer graze on the phytoplankton. Other reaction-diffusion models were also developed in [35] and [37].

In this paper, based on the models introduced in [34], [36-38], we consider three reaction-diffusion models of zooplankton-phytoplankton-nutrient interactions with instantaneous nutrient recycling. Firstly, a semi-group approach (see [7], [8], [11]) is used to discuss global existence for a model under initial and Dirichlet boundary value conditions. For the Neumann boundary value conditions, an existence theorem is established by means of a comparison principle. Comparison methods are used extensively to study ecological models, (see [3], [10], [15], [22], [23], [39], [40]). Finally, for the case with periodic coefficients, using a theorem of Liu and Pao [17], we study the existence and uniqueness of a periodic solution.

The paper is organized as follows. In the next section we describe the models. In Section 3, we study the global existence for the Dirichlet problem. In Section 4, an existence-comparison theorem is established for the Neumann problem. The existence and uniqueness of a periodic solution is investigated in Section 5 for the periodic model. The final section contains a brief discussion.

4.2 The Models

Let Ω be an open bounded set in R^3 with boundary $\partial\Omega$. $\frac{\partial}{\partial n}$ represents the outward normal derivative in $\partial\Omega$, and Δ is the Laplace operator, x is distance, t is time, $d_i > 0$ are diffusion coefficients $(i = 1, 2, 3)$. We suppose that all parameters are positive.

The first model we consider involving instantaneous nutrient recycling is given by the following set of reaction-diffusion equations:

$$\begin{aligned}
\frac{\partial N}{\partial t} &= d_1 \Delta N - aP\,\frac{N}{k+N} + (1-\delta) b Z_1 [1 - e^{-\lambda(P-P_t)}] + \gamma P + \varepsilon Z_1 + \mu Z_2 \\
\frac{\partial P}{\partial t} &= d_2 \Delta P + aP\,\frac{N}{k+N} - b Z_1 [1 - e^{-\lambda(P-P_t)}] - \gamma P \\
\frac{\partial Z_1}{\partial t} &= d_3 \Delta Z_1 + \delta b Z_1 [1 - e^{-\lambda(P-P_t)}] + \Phi Z_2 e^{-(\frac{t-t_2}{\sigma})^2} - \Phi Z_1 e^{-(\frac{t-t_1}{\sigma})^2} - \varepsilon Z_1 \\
\frac{\partial Z_2}{\partial t} &= \Phi Z_1 e^{-(\frac{t-t_1}{\sigma})^2} - \Phi Z_2 e^{-(\frac{t-t_2}{\sigma})^2} - \mu Z_2,
\end{aligned} \tag{2.1}$$

with initial value conditions

$$N(x,0) = N_0(x), \quad P(x,0) = P_0(x), \quad Z_i(x,0) = Z_{i0}(x), \quad i = 1,2, \quad x \in \Omega, \tag{2.2}$$

and the Dirichlet boundary value conditions

$$(N, P, Z_1, Z_2) = (0,0,0,0) \quad \text{on} \quad \partial\Omega \times R^+, \tag{2.3}$$

or the Neumann boundary value conditions

$$(\frac{\partial N}{\partial n}, \frac{\partial P}{\partial n}, \frac{\partial Z_1}{\partial n}, \frac{\partial Z_2}{\partial n}) = (0,0,0,0) \quad \text{on} \quad \partial\Omega \times R^+. \tag{2.4}$$

The homogeneous Neumann boundary value conditions (2.4) can be interpreted as a "no flux" condition (i.e. there is no migration of any of the populations across the boundary of habitat), whereas the homogeneous Dirichlet condition (2.3) is to be considered as a condition under which none of the three species can exist on the boundary of the habitat.

The growth rate of phytoplankton (P) expressed in terms of uptake of the biologically limiting nutrient (N) is described by the Michaelis-Menten function

$$a \frac{N}{k+N},$$

where a is the maximum uptake rate of the nutrient by phytoplankton P and k is a half-saturation constant (i.e. the concentration of N supporting half the maximum uptake rate).

The grazing of herbivorous (Z_1) upon the phytoplankton is assumed to follow a modified Ivlev function

$$g(P, Z_1) = \begin{cases} bZ_1[1 - e^{-\lambda(P-P_t)}]; & P > P_t \\ 0; & P \leq P_t, \end{cases}$$

where b is the maximum rate of herbivore grazing, λ is the Ivlev constant, i.e. the rate at which saturation is achieved with increasing phytoplankton level (per unit concentration), and P_t is the threshold concentration of P below which the grazing behaviour of the herbivores ceases. Actually, we set $b = 0$ if $P < P_t$.

During consumption, only a fraction of the biomass removed from the resources compartment, δ $(\delta \leq 1)$, is assumed to be assimilated by the consumer, the remainder goes directly to the dissolved nutrient. Besides the loss related to consumption, a second phytoplankton loss term, $-\gamma P$, represents loss due to extracellular release and senescent cell autolysis and sinking.

In many oceanic areas the herbivores' trophic level is composed of vertically migrating copepods and euphausiids. Large concentrations of these nocturnally feeding animals may impose a highly time-dependent grazing stress on the plankton. Not every individual species resides continuously in the euphatic zone. Therefore the herbivore community is divided into two fractions, Z_1 and Z_2. Z_1 is that fraction of Z located in the euphatic zone at time t. Z_2 is the remaining portion of Z which resides at the lower depths. ε is the metabolic excretion rate of the animals while feeding at the surface, μ is the excretion rate while at depth. Time t_2 is the point within the day about which ascent into the surface waters is centered (usually sunset), and t_1 is the point (after dawn) about which descent from the surface is centered. Parameter σ is the fraction of the day over which the migrational transition takes place. Parameter Φ allows one to adjust the fraction of the herbivore community which undergoes migration to fit an oceanic area's night/day ratio.

There is a continuous transfer of nutrient from the surface layers to depth by vertically migrating, metabolite excreting animals. The surface layers become depleted of nutrient if there is no resupply by vertical diffusion or upwelling. We assume that the resupply of nutrient necessary to balance the vertical loss terms is

$$(1-\delta)bZ_1[1-e^{-\lambda(P-P_t)}]+\gamma P+\varepsilon Z_1+\mu Z_2,$$

i.e. the instantaneous nutrient recycling terms.

In the second model, we suppose that all the phytoplankton removed through zooplankton predation is assimilated by zooplankton, i.e. $\delta = 1$. The model takes the following form

$$
\begin{aligned}
\frac{\partial N}{\partial t} &= d_1 \Delta N - aP\,\frac{N}{k+N} + \gamma P + \varepsilon Z_1 + \mu Z_2 \\
\frac{\partial P}{\partial t} &= d_2 \Delta P + aP\,\frac{N}{k+N} - bZ_1[1 - e^{-\lambda(P-P_t)}] - \gamma P \\
\frac{\partial Z_1}{\partial t} &= d_3 \Delta Z_1 + bZ_1[1 - e^{-\lambda(P-P_t)}] + \Phi Z_2 e^{-(\frac{t-t_2}{\sigma})^2} - \Phi Z_1 e^{-(\frac{t-t_1}{\sigma})^2} - \varepsilon Z_1 \\
\frac{\partial Z_2}{\partial t} &= \Phi Z_1 e^{-(\frac{t-t_1}{\sigma})^2} - \Phi Z_1 e^{-(\frac{t-t_2}{\sigma})^2} - \mu Z_2,
\end{aligned}
\tag{2.5}
$$

with conditions (2.2) and (2.4). All parameters are the same as in system (2.1).

In order to model the third system, we suppose that Z_2 is removed temporarily from the biological dynamics. Usually, uptake of nutrients by phytoplankton exhibits diel periodicity, as uptake is indirectly coupled to light-dependent phytosynthesis (Wroblewski and O'Brien [36]). To simulate this behaviour, the nutrient uptake term is multiplied by the function

$$\rho(t) = \frac{\pi}{2\theta} \sin \frac{\pi t}{\theta} ,$$

where θ is the daylight fraction of a day and t is time in hours. When $\rho(t) \leq 0$, one sets $\rho(t) = 0$ to simulate no growth at night. Note that $\rho(t)$ is a 2θ periodic function, and if N is constant, the total uptake over one day is the same with or without multiplication by this function, since

$$\int_0^\theta \rho(t) dt = 1.$$

The function acts to condense the daily phytoplankton growth into the θ fraction of a nondimensional day, assuming dawn begins at $t = 0$.

Now the third model has the following form

$$\begin{aligned}\frac{\partial N}{\partial t} &= \frac{\partial^2 N}{\partial x^2} - a\rho(t)\,\frac{NP}{k+N} + (1-\delta)bZ[1-e^{-\lambda(P-P_t)}] + \gamma P + \varepsilon Z\\ \frac{\partial P}{\partial t} &= \frac{\partial^2 P}{\partial x^2} + a\rho(t)\,\frac{NP}{k+N} - bZ[1-e^{-\lambda(P-P_t)}] - \gamma P\\ \frac{\partial Z}{\partial t} &= \frac{\partial^2 Z}{\partial x^2} + \delta bZ[1-e^{-\lambda(P-P_t)}] - \varepsilon Z,\end{aligned} \tag{2.6}$$

for $(t,x) \in D = (0,2\theta)\times(0,x_0)$, under the Dirichlet boundary value conditions

$$(N,P,Z) = (0,0,0) \quad \text{when} \quad x=0,\ x=x_0,\ t\in[0,2\theta]. \tag{2.7}$$

Notice that upon neglecting the effort of diffusion,

$$\frac{\partial N}{\partial t} + \frac{\partial P}{\partial t} + \frac{\partial Z}{\partial t} = 0,$$

i.e. the total amount of biological limiting nutrient in the oceanic region is conserved in these models.

For the plankton-nutrient models neglecting diffusion, we refer to [1], [26], [27], [38].

4.3 Global Existence

In view of the special form of the reaction terms in system (2.1), we know that

$$\Sigma = \{(N,P,Z_1,Z_2):\ N\geq 0,\ P\geq 0,\ Z_1\geq 0,\ Z_2\geq 0\}$$

is an invariant region for system (2.1), [28].

Denote

$$U(t) = \big(N(t), P(t), Z_1(t), Z_2(t)\big),$$

and define a space

$$X = \{L^2(\Omega)\}^4$$

with norm

$$\|U\| = (\|N\|_2^2 + \|P\|_2^2 + \|Z_1\|_2^2 + \|Z_2\|_2^2)^{1/2}$$

for any $U = (N, P, Z_1, Z_2) \in X$, where $\| \cdot \|_2$ denotes the usual norm in $L^2(\Omega)$. Clearly X is a Banach space.

In the Banach space X, system (2.1) can be considered as an evaluation in the following form

$$\frac{dU}{dt} = AU + F(t, U), \quad U(0) = U_0, \tag{3.1}$$

where

$$U_0 = \big(N_0(x), P_0(x), Z_{10}(t), Z_{20}(x)\big),$$

$$A = \begin{pmatrix} A_1 & 0 & 0 & 0 \\ 0 & A_2 & 0 & 0 \\ 0 & 0 & A_3 & 0 \\ 0 & 0 & 0 & A_4 \end{pmatrix} = \begin{pmatrix} d_1\Delta & 0 & 0 & 0 \\ 0 & d_2\Delta - \gamma & 0 & 0 \\ 0 & 0 & d_3\Delta - \varepsilon & 0 \\ 0 & 0 & 0 & -\mu \end{pmatrix}, \tag{3.2}$$

$$F(t, U) = \begin{pmatrix} -aP\,\frac{N}{k+N} + (1-\delta)bZ_1[1 - e^{-\lambda(P-P_t)}] + \gamma P + \varepsilon Z_1 + \mu Z_2 \\ aP\,\frac{N}{k+N} - bZ_1[1 - e^{-\lambda(P-P_t)}] \\ \delta bZ_1[1 - e^{-\lambda(P-P_t)}] + \Phi Z_2 e^{-(\frac{t-t_2}{\sigma})^2} - \Phi Z_1 e^{-(\frac{t-t_1}{\sigma})^2} \\ \Phi Z_1 e^{-(\frac{t-t_1}{\sigma})^2} - \Phi Z_2 e^{-(\frac{t-t_2}{\sigma})^2} \end{pmatrix}, \tag{3.4}$$

and denote

$$D(A_i) = \{u \in L^2(\Omega),\ u|_{\partial\Omega} = 0,\ A_i u \in L^2(\Omega)\}.$$

It is well known that $D(A_i) \subseteq H_0^1(\Omega)$ and $D(A_i)$ is dense in $L^2(\Omega)$.

Suppose Y and Z are Banach spaces and $T : Y \to Z$ is a linear bounded operator. Let $\|T\|_{Y,Z}$ denote the norm of T. For a closed operator T, let $\rho(T)$ denote the resolvent set of T, consisting of all complex numbers μ for which $(\mu I - T)^{-1}$ is a bounded operator. Further, let $\sigma(T)$ denote the spectrum of T, consisting of the complement of $\rho(T)$ in C, and let $R(\mu, T) = (\mu I - T)^{-1}$ denote the resolvent operator of T. Firstly we recall the following definitions of Henry [8].

We call a linear operator A in a Banach space X a *sectorial operator* if it is a closed densely defined operator such that for $\theta \in (0, \frac{\pi}{2})$, $M \geq 1$ and $a \in R$, the sector

$$S_{a,\theta} = \{\mu \in C :\ \theta \leq |\arg(\mu - a)| \leq \pi,\ \mu \neq a\}$$

is in the resolvent set of A and

$$\|R(\mu, A)\| \leq \frac{M}{|\mu - a|} \quad \text{for all} \quad \mu \in S_{a,\theta}.$$

We know from [8] that if A is a bounded linear operator on a Banach space, then A is sectorial, and if A is a self adjoint densely defined operator in a Hilbert space which is bounded below, then A is sectorial.

An *analytic semigroup* on a Banach space X is a family of continuous linear operators on X, $\{T(t);\ t \geq 0\}$, satisfying

(i) $T(0) = I, \quad T(t)T(s) = T(t+s)$ for $t \geq 0,\ s \geq 0$;

(ii) $T(t)x \to x$ as $t \to 0^+$ for each $x \in X$;

(iii) $t \to T(t)x$ is real analytic on $0 < t < \infty$ for each $x \in X$.

The infinitesimal generator L of this semigroup is defined by

$$Lx = \lim_{t \to 0^+} \tfrac{1}{t} \{T(t)x - x\},$$

and its domain $D(L)$ consists of all $x \in X$ for which this limit (in X) exists. We usually write $T(t) = e^{Lt}$.

Lemma 3.1. *The operator A given by (3.2) generates an analytic semigroup e^{At} on X.*

Proof: Since $D(A_i) = H^2(\Omega) \cap H_0^1(\Omega)$, where $H^k(\Omega) = W^{k,2}(\Omega)$, $k \geq 0$; $H_0^k(\Omega) = W_0^{k,2}(\Omega)$, it follows that

$$D(A) = \{H^2(\Omega) \cap H_0^1(\Omega)\}^4,$$

which implies that $-A$ is a closed densely defined operator on X. Since $-A_i$ is a self adjoint densely defined operator in $L^2(\Omega)$ and is bounded below, $-A_i$ is a sectorial operator on X_i. Hence there exist $M_i \geq 1$, $a_i \in R$ and $\theta_i \in (0, \frac{\pi}{2})$ such that

$$\rho(-A_i) \supset S_{a_i,\theta_i} = \{\mu :\ \theta_i \leq |\arg(\mu - a_i)| \leq \pi\}$$

and

$$\|R(\mu_1 - A_i)\|_{L^2,L^2} \leq \frac{M_i}{|\mu - a_i|} \quad \text{for all} \quad \mu \in S_{a_i,\theta_i},\ i = 1,2,3,4.$$

$-\lambda_0^i$ is the largest eigenvalue of A_i. Let a_i be the smallest eigenvalue λ_0^i of $(-A_i)$ and define $\gamma_0 = \min\limits_{1 \le i \le 4} \{\lambda_0^i\}$, $\theta = \max\limits_{1 \le i \le 4} \{\theta_i\}$. Then by (3.2), we have

$$R(\mu, -A) = \begin{pmatrix} R(\mu, -A_i) & 0 & 0 & 0 \\ 0 & R(\mu, -A_2) & 0 & 0 \\ 0 & 0 & R(\mu, -A_3) & 0 \\ 0 & 0 & 0 & R(\mu, -A_4) \end{pmatrix}$$

for all $\mu \in \rho(A)$. Hence $\rho(-A) \supset S_{\gamma_0,\theta}$ and there exists $M_0 \ge 1$ such that

$$\|R(\mu, -A)\| \le \frac{M_0}{|\mu - \gamma_0|} \quad \text{for all} \quad \mu \in S_{\gamma_0,\theta},$$

which means $-A$ is a sectorial operator on X, by Theorem 1.3.4 of [8], and so A generates an analytic semigroup e^{At} on X and satisfies

$$\|e^{At}\| \le Me^{-\gamma_0 t} \quad \text{for a suitable constant} \quad M.$$

□

Suppose A is a sectorial operator in a Banach space X and $\operatorname{Re} \sigma(A) > 0$, then for any $\alpha > 0$,

$$A^{-\alpha} = \frac{1}{\Gamma(\alpha)} \int_0^\infty t^{\alpha-1} e^{-At} dt,$$

A^α is the inverse of $A^{-\alpha}$, A^0 is the identity on X and $D(A^\alpha) = R(A^{-\alpha})$. Also we define for each $\alpha \ge 0$

$$X^\alpha = D(A_i^\alpha) \quad \text{with the graph norm,}$$

$$\|x\|_\alpha = \|A_1^\alpha x\|, \quad x \in X^\alpha,$$

where $A_1 = A + aI$ with a chosen so that $\operatorname{Re}\sigma(A_1) > 0$.

We say that a set $\Omega \subset R^n$ has the C^m*-extension property,* if there is an extension map $E : C_c^m(\overline{\Omega}) \to C_c^m(R^n)$, so that $E(\varphi)$ restricted to $\overline{\Omega}$ is φ, such that for the norms of any of the spaces C^ν or $W^{k,q}$ $(0 \le \nu,\ k \le m$ and $1 \le q < \infty)$ there exists a constant $B > 0$ with

$$B^{-1}\|\varphi\|_\Omega \le \|E(\varphi)\|_{R^n} \le B\|\varphi\|_\Omega.$$

If Ω is bounded and $\partial\Omega$ is a C^m hypersurface separating Ω from $R^n \backslash \Omega$, then such an extension map can be easily constructed [7].

Lemma 3.2. *Let* $0 \le \alpha \le 1$. *Suppose* X^α *is a Banach space with* $-A$ *instead of* A. *Assume* $\alpha = \alpha_0 > \frac{3}{4}$, *then*

$$X^{\alpha_0} \subset \{L^\infty(\Omega) \cap W^{1,2}(\Omega)\}^4$$

continuously.

PROOF: Since

$$D(A_i) = H^2(\Omega) \cap H_0^1(\Omega) = W^{2,2}(\Omega) \cap W_0^{1,2}(\Omega), \quad i = 1, 2, 3, 4,$$

letting $A = -A_i$, $m = 2$, $p = 2$, $n = 3$, by Theorem 1.6.1 of [8], for $\alpha_0 > \frac{3}{4}$, we have

$$X^{\alpha_0} \subset C^\nu(\Omega) \quad \text{when} \quad 0 \le \nu \le \frac{4\alpha_0 - 3}{2}.$$

Taking $k = 1$, $q = 2$, Theorem 1.6.1 of [8] also implies that

$$X_i^\alpha \subset W^{1,2}(\Omega).$$

Therefore we have that

$$X_i^{\alpha_0} \subset L^\infty(\Omega) \cap W^{1,2}(\Omega), \quad i = 1,2,3,4.$$

It is easy to prove that the inclusion is continuous, completing the proof.

□

Lemma 3.3. *Fix* $0 \le \alpha \le 1$, $-\infty < t_0 < T_0 \le \infty$ *and assume* V *is an open set in* X^α. *Then the nonlinear operator* $F : [t_0, T_0) \times V \to X$ *defined by (3.3) is locally Hölder continuous in* t *and locally Lipschitzian in* U. *More precisely, for every* $(t,U) \in [t_0,T_0) \in V$, *there exists* $L > 0$, $\delta > 0$ *and* $\theta \in (0,1]$ *such that*

$$\|F(s_1,U_1) - F(s_2,U_2)\| \le L(|s_1 - s_2|^\theta + \|U_1 - U_2\|_\alpha),$$

whenever $t_0 \le s_i < T_0$, $U_i \in V$ *and* $|s_i - t| + \|U_i - U\|_\alpha < \delta$ *for* $i = 1,2$.

PROOF: Let $U_i = \{N^{(i)}, P^{(i)}, Z_1^{(i)}, Z_2^{(i)}\}$, $i = 1,2$, and

$$F(t,U) = \begin{pmatrix} f_1(U) \\ f_2(U) \\ f_3(t,U) \\ f_4(t,U) \end{pmatrix}, \quad F(s_1,U_1) - F(s_2,U_2) = \begin{pmatrix} f_1(U_1) - f_1(U_2) \\ f_2(U_1) - f_2(U_2) \\ f_3(s_1,U_1) - f_3(s_2,U_2) \\ f_4(s_1,U_1) - f_4(s_2,U_2) \end{pmatrix}.$$

By (3.3), it suffices to prove that for any U_i with $N^{(i)} \ge -\frac{k}{2}$ and $\|U_i\|_{\alpha_0} \le R^*$,

$R^* > 0$, $i = 1,2$,

$$\|F(s_1,U_1) - F(s_2,U_2)\| \le L(|s_1 - s_2|^\theta + \|U_1 - U_2\|_{\alpha_0}), \tag{3.4}$$

where L depends only on R^* and the parameters in F. By Lemma 3.2, there exists R_1 depending on R^* such that

$$|U_i|_\infty \leq R_1.$$

From (3.3), we have

$$\begin{aligned} |f_1(U_1) - f_2(U_2)| \leq {} & (a+\gamma)|P^{(1)} - P^{(2)}| + [(1-\delta)b + \varepsilon]\, |Z_1^{(1)} - Z_1^{(2)}| \\ & + \mu|Z_2^{(1)} - Z_2^{(2)}| + ak\, \left|\frac{P^{(1)}}{k+N^{(1)}} - \frac{P^{(2)}}{k+N^{(2)}}\right| \\ & + (1-\delta)b\, |e^{-\lambda(P^{(1)}-P_t)} - e^{-\lambda(P^{(2)}-P_t)}|. \end{aligned}$$

Since

$$\left|\frac{P^{(1)}}{k+N^{(1)}} - \frac{P^{(2)}}{k+N^{(2)}}\right| \leq \frac{2}{k}\, |P^{(1)} - P^{(2)}| + \frac{4R_1}{k^2}\, |N^{(1)} - N^{(2)}|,$$

$$|e^{-\lambda(P^{(1)}-P_t)} - e^{-\lambda(P^{(2)}-P_t)}| \leq \lambda|P^{(1)} - P^{(2)}|,$$

it follows that

$$\begin{aligned} |f_1(U_1) - f_2(U_2)| \leq {} & [3a + \gamma + (1-\delta)b\lambda]\, |P^{(1)} - P^{(2)}| + \frac{4R_1 a}{k}\, |N^{(1)} - N^{(2)}| \\ & + [(1-\delta)b + \varepsilon]\, |Z_1^{(1)} - Z_1^{(2)}| + \mu|Z_2^{(1)} - Z_2^{(2)}|. \end{aligned}$$

Similarly,

$$|f_2(U_1) - f_2(U_2)| \leq \frac{4R_1 a}{k}\, |N^{(1)} - N^{(2)}| + [3a + b\lambda]\, |P^{(1)} - P^{(2)}| + b|Z_1^{(1)} - Z_1^{(2)}|.$$

Now we have that

$$
\begin{aligned}
|f_3(s_1,U_1) - f_3(s_2,U_2)| \le\ & \delta b|Z_1^{(1)} - Z_1^{(2)}| + \delta b\lambda|P^{(1)} - P^{(2)}| \\
& + \Phi[|Z_1^{(1)} - Z_1^{(2)}| + |Z_1|\, |e^{-(\frac{s_1-t_2}{\sigma})^2} - e^{-(\frac{s_2-t_2}{\sigma})^2}|] \\
& + \Phi[|Z_2^{(1)} - Z_2^{(2)}| + |Z_2|\, |e^{-(\frac{s_1-t_1}{\sigma})^2} - e^{-(\frac{s_2-t_1}{\sigma})^2}|] \\
\le\ & \frac{4R_1\Phi}{\sigma^2}\, |s_1 - s_2| + \delta b\lambda|P^{(1)} - P^{(2)}| \\
& + (\delta b + \Phi)|Z_1^{(1)} - Z_1^{(2)}| + \Phi|Z_2^{(1)} - Z_2^{(2)}|.
\end{aligned}
$$

Similary

$$
\|f_4(s_1,U_1) - f_4(s_2,U_2)| \le \frac{4R_1\Phi}{\sigma^2}\, |s_1 - s_2| + \Phi|Z_1^{(1)} - Z_1^{(2)}| + \Phi|Z_2^{(1)} - Z_2^{(2)}|.
$$

By Theorem 1.6.1 of [8], we get (3.4), which implies that F is locally Hölder continuous in t and locally Lipschitz continuous in x.

□

Lemma 3.4 ([8], Theorem 3.3.3 and 3.5.2). *Assume* A *is a sectorial operator,*
$0 \le \alpha \le 1$ *and* $f : W \to X$, W *is an open set of* $R \times X^\alpha$, $f(t,x)$ *is locally Hölder continuous in* t *and locally Lipschitz continuous in* x. *Then for any* $(t_0, x_0) \in W$ *there exists* $T = T(t_0,x_0) > 0$ *such that the initial value problem*

$$
\frac{dx}{dt} + Ax = f(t,x), \quad t > t_0, \quad x(t_0) = x_0 \tag{3.5}
$$

has a unique solution on $(t_0,\ t_0 + T)$. *Furthermore, if* $\gamma < 1$, *then* $t \to \frac{dx}{dt} \in X^\gamma$ *is locally Hölder continuous for* $t_0 < t \le t_0 + T$ *with* $\| \frac{dx}{dt} \|_\gamma \le C(t - t_0)^{\alpha-\gamma-1}$ *for some constant* C.

REMARK: As shown via a counterexample by Miklačič [18], Henry's definition of a solution of equation (3.5) needs a minor modification. Here we use Miklačič's definition.

Lemma 3.5. *For any* $U_0 = \big(N_0(x), P_0(x), Z_{10}(x), Z_{20}(x)\big) \in X^\alpha$, *there exists* $T > 0$ *such that the initial value problem (3.1) has a unique classical solution* $t \to U(t) = \big(N(t), P(t), Z_1(t), Z_2(t)\big)$ *in* $[0, T)$.

PROOF: By Lemma 3.4, for $(0, U_0) \in \mathcal{D} = R_1^+ \times \{(N, P, Z_1, Z_2) \in X^\alpha,\ N \geq -\frac{k}{2}\}$, there exists $T(0, U_0) > 0$ such that (3.1) has a unique solution $U(t)$ on $(0, T)$. For $t \in (0, T)$, $\big(t, U(t)\big) \in \mathcal{D}$, $U(t) \in D(A)$. $\frac{dU(t)}{dt}$ exists and $t \to F\big(t, U(t)\big)$ is locally Hölder continuous, $\int_0^\rho \|F\big(t, U(t)\big)\|dt < \infty$ for some $\rho > 0$, $U(t)$ can be expressed as

$$U(t) = e^{At}U_0 + \int_0^t e^{A(t-s)}F\big(s, U(s)\big)ds. \tag{3.6}$$

Since $\alpha_0 = \frac{3}{4} < 1$, by Lemma 3.4, when $t > 0$, $t \to \frac{dU(t)}{dt} \in X^{\alpha_0}$ is locally Hölder continuous, so $(t, x) \to U(t, x)$ and $\frac{\partial U(t,x)}{\partial t}$ are also continuous for $0 < t < T$ and $x \in \overline{\Omega}$. Since $U(t) \in D(A)$ implies $U(t) \in \{W^{2,2}(\Omega) \cap W_0^{1,2}(\Omega)\}^4$, by the Embedding Theorem, there exists $\nu > 0$ such that $U(t) \in \{C^\nu(\Omega)\}^4$, and hence $F\big(t, U(t)\big) \in \{C^\nu(\Omega)\}^4$. Therefore we have that $U(x, t) \in C^{2+\nu}(\Omega)$, which means that for $t > 0$, $(t, x) \to U(t, x)$ is continuously differentiable in t, twice continuously differentiable in x, i.e. we get a classical solution.

□

Theorem 3.6. *For any* $U_0 \in X^{\alpha_0}$, $U_0 \geq 0$, *the corresponding solution exists* *globally and is nonnegative for all* $t \geq 0$.

PROOF: We consider the system on Σ, so $U_0 \geq 0$ implies that $U(t) \geq 0$ for $0 \leq t < T$.

From the proof of Lemma 3.5, we have (3.6). Since $F(t,U)$ is locally Lipschitz continuous, we obtain that

$$\|U(t)\|_{\alpha_0} \leq \|e^{At}U_0\|_{\alpha_0} + \int_0^t \|e^{A(t-s)}\| \cdot L\|U(s)\|_{\alpha_0} ds. \tag{3.7}$$

By Theorem 1.4.3 of [8], $\operatorname{Re}\sigma(-A) > \gamma_0 > 0$, $\alpha_0 = \frac{3}{4} > 0$, so there exists $C_{\alpha_0} < \infty$ such that

$$\|e^{At}U_0\|_{\alpha_0} \leq \|(-A)^{\alpha_0}e^{At}\| \cdot \|U_0\| \leq C_{\alpha_0}t^{-\alpha_0}e^{-\gamma_0 t}\|U_0\|,$$

and

$$\|e^{A(t-s)}\| \leq M_1 e^{-\gamma_0(t-s)}.$$

Hence (3.7) implies that

$$\|U(t)\|_{\alpha_0} \leq C_{\alpha_0}t^{-\alpha_0}e^{-\gamma_0 t}\|U_0\| + \int_0^t M_1 e^{-\gamma_0(t-s)}\|U(s)\|_{\alpha_0} ds,$$

which can be written as

$$e^{\gamma_0 t}\|U(t)\|_{\alpha_0} \leq C_{\alpha_0}t^{-\alpha_0}\|U_0\| + \int_0^t M_1 e^{\gamma_0 s}\|U(s)\|_{\alpha_0} ds.$$

By Gronwall's inequality, there exists a positive constant M such that

$$\|U(t)\|_{\alpha_0} \leq Mt^{-\alpha_0}e^{-\gamma_0 t}\|U_0\| \quad \text{for all} \quad t \in (0,T), \tag{3.8}$$

which provides an estimate for $U(t)$. The global existence and nonnegativity of $U(t)$ follow in a standard way, together with the validity of (3.7) on R^+.

□

Now, we discuss the existence of nonnegative and bounded solution of (2.1)–(2.3). Let λ_0 denote the principal eigenvalue of Laplace operator Δ on Ω with homogeneous Dirichlet boundary value conditions. Clearly $\lambda_0 < 0$.

Theorem 3.7. *For any* $U_0 \in X^{\alpha_0}$ *with* $U_0 \geq 0$, *the Dirichlet problem (2.1)–(2.3) has a unique classical solution which exists globally and is nonnegative and bounded in the sense of* L_∞.

PROOF: By Theorem 3.6, we only need to prove the boundedness. By the expression of A, take

$$-\gamma_0 = \max\colon \{d_1\lambda_0, d_2\lambda_0 - \gamma,\ d_3\lambda_0 - \varepsilon, -\mu\} < 0.$$

For $U_0 \in X^{\alpha_0}$, we know $U(t) \in X^{\alpha_0}$. By Lemma 3.2, $X^{\alpha_0} \hookrightarrow \{L_\infty(\Omega)\}^4$ continuously, together with (3.8) imply that

$$|U(t)|_{\{L_\infty\}^4} \leq Mt^{-\alpha_0}e^{-\gamma_0 t}\|U_0\| \quad \text{for} \quad t > 0. \tag{3.9}$$

This proves the boundedness and thus completes the proof of the theorem.

□

An equilibrium solution $0 = (0,0,0,0)$ of (2.1)–(2.3) is said to be ***globally stable***, if for any $U_0 \in X^{\alpha_0}$ with $U_0 \geq 0$, the solution $U(t)$ of (2.1)–(2.3) satisfies $\lim\limits_{t\to\infty} U(t) = 0$ uniformly in x in the sense of L_∞.

Since $-\gamma_0 < 0$, by (3.9) we have the following result

Theorem 3.8. *The equilibrium solution* $(0,0,0,0)$ *of (2.1)–(2.3) is globally stable.*

4.4 Comparison Theorems

In this section, we first consider the more general system

$$\begin{aligned} u_{1t} - d_1 \Delta u_1 &= f_1(u_1, u_2, u_3, u_4) \\ u_{2t} - d_2 \Delta u_2 &= f_2(u_1, u_2, u_3) \\ u_{3t} - d_3 \Delta u_3 &= f_3(t, u_2, u_3, u_4) \\ u_{4t} \qquad\quad &= f_4(t, u_3, u_4) \end{aligned} \quad \text{in} \quad R^+ \times \Omega, \tag{4.1}$$

with the boundary conditions

$$B_i[u_i] = \alpha_i(x) u_i + \beta_i(x) \frac{\partial u_i}{\partial n} = h_i(x), \quad i = 1,2,3,4 \quad \text{on} \quad \partial\Omega \times R^4, \tag{4.2}$$

and initial conditions

$$u_i(x,0) = u_{i0}(x), \quad i = 1,2,3,4 \quad \text{on} \quad \Omega, \tag{4.3}$$

where Ω is a bounded domain in R^n. $\partial\Omega$ is the boundary of Ω. α_i, β_i, and u_{i0} are smooth nonnegative functions with respect to their variables for $u_k \geq 0$, $i, k = 1,2,3$. In addition, in order to employ the monotone argument to establish an existence-comparison theorem in terms of upper and lower solutions for (4.1)–(4.3), we require the following assumptions on f_i for $u_i \geq 0$, $i =$

1, 2, 3, 4.

$$\begin{array}{lll} \frac{\partial f_1}{\partial u_2} \le 0, & \frac{\partial f_1}{\partial u_3} \ge 0, & \frac{\partial f_1}{\partial u_4} \ge 0 \\ \frac{\partial f_2}{\partial u_1} \ge 0, & \frac{\partial f_2}{\partial u_3} \le 0 & \\ \frac{\partial f_3}{\partial u_2} \ge 0, & \frac{\partial f_3}{\partial u_4} \ge 0 & \\ \frac{\partial f_4}{\partial u_3} \ge 0. & & \end{array} \tag{4.4}$$

Definition 4.1. Let $Q_T = \Omega \times (0,T)$, $S_T = \partial\Omega \times (0,T)$ and $T < \infty$, but can be chosen as large as we wish. An ordered pair of smooth functions $\overline{u} = (\overline{u}_1, \overline{u}_2, \overline{u}_3, \overline{u}_4)$ and $\underline{u} = (\underline{u}_1, \underline{u}_2, \underline{u}_3, \underline{u}_4)$ are called *upper and lower solutions* of (4.1)–(4.3), respectively, if they satisfy the following inequalities

$$\left.\begin{array}{ll} \overline{u}_{1t} - k_1\Delta\overline{u}_1 & \ge f_1(\overline{u}_1, \underline{u}_2, \overline{u}_3, \overline{u}_4) \\ \overline{u}_{2t} - k_2\Delta\overline{u}_2 & \ge f_2(\overline{u}_1, \overline{u}_2, \underline{u}_3) \\ \overline{u}_{3t} - k_3\Delta\overline{u}_3 & \ge f_3(t, \overline{u}_2, \overline{u}_3, \overline{u}_4) \\ \overline{u}_{4t} & \ge f_4(t, \overline{u}_3, \overline{u}_4), \end{array}\right\} \quad in \quad Q_T \tag{4.5}$$

$$\left.\begin{array}{ll} \underline{u}_{1t} - k_1\Delta\underline{u}_1 & \le f_1(\underline{u}_1, \overline{u}_2, \underline{u}_3, \underline{u}_4) \\ \underline{u}_{2t} - k_2\Delta\underline{u}_2 & \le f_2(\underline{u}_1, \underline{u}_2, \overline{u}_3) \\ \underline{u}_{3t} - k_3\Delta\underline{u}_3 & \le f_3(t, \underline{u}_2, \underline{u}_3, \underline{u}_4) \\ \underline{u}_{4t} & \le f_4(t, \underline{u}_3, \underline{u}_4), \end{array}\right\} \quad in \quad Q_T \tag{4.6}$$

$$B_i[\overline{u}_i] \ge h_i(x) \ge B_i[\underline{u}_i], \qquad i = 1,2,3,4 \quad on \quad S_T, \tag{4.7}$$

$$\overline{u}_i(x,0) \ge u_{i0}(x) \ge \underline{u}_i(x,0), \quad i = 1,2,3,4 \quad on \quad \Omega. \tag{4.8}$$

Suppose $\overline{u}$ and $\underline{u}$ exist. Denote

$$\Sigma_1 = \{(u_1, u_2, u_3, u_4) \in R^4 : \inf_{(x,t)\in Q_T} \underline{u}_i(x,t) \le u_i \le \sup_{(x,t)\in Q_T} \overline{u}_i(x,t),\ i = 1,2,3,4\},$$

$$M_i = \sup_{\Sigma_1} \{|\frac{\partial f_i}{\partial u_i}|\}, \quad i = 1,2,3,4.$$

We construct a sequence $\{\overline{u}^{(k)}\}$ with $\overline{u}^{(0)} = \overline{u}$ as follows:

$$\begin{aligned}
\overline{u}_{1t}^{(k)} - d_1\Delta\overline{u}_1^{(k)} + M_1\overline{u}_1^{(k)} &= M_1\overline{u}_1^{(k-1)} + f_1(\overline{u}_1^{(k-1)}, \underline{u}_2^{(k-1)}, \overline{u}_3^{(k-1)}, \overline{u}_4^{(k-1)}) \\
\overline{u}_{2t}^{(k)} - d_2\Delta\overline{u}_2^{(k)} + M_2\overline{u}_2^{(k)} &= M_2\overline{u}_2^{(k-1)} + f_2(\overline{u}_1^{(k-1)}, \overline{u}_2^{(k-1)}, \underline{u}_3^{(k-1)}) \\
\overline{u}_{3t}^{(k)} - d_3\Delta\overline{u}_3^{(k)} + M_3\overline{u}_3^{(k)} &= M_3\overline{u}_3^{(k-1)} + f_3(t, \overline{u}_2^{(k-1)}, \overline{u}_3^{(k-1)}, \overline{u}_4^{(k-1)}) \\
\overline{u}_{4t}^{(k)} + \qquad\qquad M_4\overline{u}_4^{(k)} &= M_4\overline{u}_4^{(k-1)} + f_4(t, \overline{u}_3^{(k-1)}, \overline{u}_4^{(k-1)}),
\end{aligned} \tag{4.9}$$

and a sequence $\{\underline{u}^{(k)}\}$ with $\underline{u}^{(c)} = \underline{u}$ as follows:

$$\begin{aligned}
\underline{u}_{1t}^{(k)} - d_1\Delta\underline{u}_1^{(k)} + M_1\underline{u}_1^{(k)} &= M_1\underline{u}_1^{(k-1)} + f_1(\underline{u}_1^{(k-1)}, \overline{u}_2^{(k-1)}, \underline{u}_3^{(k-1)}, \underline{u}_4^{(k-1)}) \\
\underline{u}_{2t}^{(k)} - d_2\Delta\underline{u}_2^{(k)} + M_2\underline{u}_2^{(k)} &= M_2\underline{u}_2^{(k-1)} + f_2(\underline{u}_1^{(k-1)}, \underline{u}_2^{(k-1)}, \overline{u}_3^{(k-1)}) \\
\underline{u}_{3t}^{(k)} - d_3\Delta\underline{u}_3^{(k)} + M_3\underline{u}_3^{(k)} &= M_3\underline{u}_3^{(k-1)} + f_3(t, \underline{u}_2^{(k-1)}, \underline{u}_3^{(k-1)}, \underline{u}_4^{(k-1)}) \\
\underline{u}_{4t}^{(k)} + \qquad\qquad M_4\underline{u}_4^{(k)} &= M_4\underline{u}_4^{(k-1)} + f_4(t, \underline{u}_3^{(k-1)}, \underline{u}_4^{(k-1)}),
\end{aligned} \tag{4.10}$$

for $(x,t) \in Q_T$ and

$$B_i[\overline{u}_i^{(k)}] = h_i(x) = B_i[\underline{u}_i^{(k)}], \qquad i = 1,2,3,4, \quad (x,t) \in S_T, \tag{4.11}$$

$$\overline{u}_i^{(k)}(x,0) = u_{i0}(x) = \underline{u}_i^{(k)}(x,0), \quad i = 1,2,3,4 \qquad x \in \Omega. \tag{4.12}$$

By using a standard technique [23], we can establish the following existence-comparison theorem.

Theorem 4.2. *Suppose that the assumptions (4.4) hold and there exists a pair of upper and lower solutions* $\overline{u} = (\overline{u}_1, \overline{u}_2, \overline{u}_3, \overline{u}_4)$ *and* $\underline{u} = (\underline{u}_1, \underline{u}_2, \underline{u}_3, \underline{u}_4)$ *satisfying* $\underline{u}_i \leq \overline{u}_i$, $i = 1, 2, 3, 4$. *Then the sequences* $\{\overline{u}^{(k)}\}$ *and* $\{\underline{u}^{(k)}\}$ *obtained from (4.9)–(4.12) convergence monotonically from above and below, respectively to a unique solution* $u = (u_1, u_2, u_3, u_4)$ *of (4.1)–(4.3) such that*

$$\underline{u}_i(x,t) \leq u_i(x,t) \leq \overline{u}_i(x,t), \quad i = 1,2,3,4, \quad (x,t) \in Q_T. \tag{4.13}$$

Now we consider system (2.5) under the initial value conditions (2.2) and Neumann boundary value conditions (2.4). Denote

$$\begin{aligned} f_1(N,P,Z_1,Z_2) &= -aP\,\frac{N}{k+N} + \gamma P + \varepsilon Z_1 + \mu Z_2, \\ f_2(N,P,Z_1) &= aP\,\frac{N}{k+N} - bZ_1[1 - e^{-\lambda(P-P_t)}] - \gamma P, \\ f_3(t,P,Z_1,Z_2) &= bZ_1[1 - e^{-\lambda(P-P_t)}] + \Phi Z_2 e^{-(\frac{t-t_2}{\sigma})^2} - \Phi Z_1 e^{-(\frac{t-t_1}{\sigma})^2} - \varepsilon Z_1 \\ f_4(t,Z_1,Z_2) &= \Phi Z_1 e^{-(\frac{t-t_1}{\sigma})^2} - \Phi Z_2 e^{-(\frac{t-t_2}{\sigma})^2} - \mu Z_2. \end{aligned}$$

We assume that $a > \gamma$. If there is enough nutrient, i.e. N is sufficiently large, then $\frac{\partial f_1}{\partial P} \leq 0$, and hence f_i $(i = 1,2,3,4)$ satisfy all conditions in (4.4). In order to obtain a pair of upper and lower solutions of system (2.5), we set

$$\widehat{N} = \sup_{\overline{\Omega}} N_0(x), \quad \widehat{P} = \sup_{\overline{\Omega}} P_0(x), \quad \widehat{Z}_i = \sup_{\overline{\Omega}} Z_{i0}(x), \quad i = 1,2. \tag{4.16}$$

Consider the following initial value problem of ODEs.

$$\begin{aligned}
\frac{dN(t)}{dt} &= \gamma P + \varepsilon Z_1 + \mu Z_2, & N(0) &= \widehat{N} \\
\frac{dP(t)}{dt} &= (a-\gamma)P, & P(0) &= \widehat{P} \\
\frac{dZ_1(t)}{dt} &= (b-\varepsilon)Z_1 + \Phi Z_2, & Z_1(0) &= \widehat{Z}_1 \\
\frac{dZ_2(t)}{dt} &= \Phi Z_1 - \mu Z_2, & Z_2(0) &= \widehat{Z}_2.
\end{aligned} \tag{4.15}$$

It is easy to obtain

$$\begin{aligned}
N(t) &= \frac{1}{\lambda_3}\,\gamma\widehat{P}e^{\lambda_3 t} + \frac{1}{\lambda_1}\,(\varepsilon m_{11}\widehat{Z}_1 + \mu m_{21}\widehat{Z}_2)e^{\lambda_2 t} + \frac{1}{\lambda_3}(\varepsilon m_{12}\widehat{Z}_1 + \mu m_{22}\widehat{Z}_2)e^{\lambda_2 t} + \widehat{N}, \\
P(t) &= \widehat{P}e^{\lambda_3 t}, \\
Z_1(t) &= m_{11}\widehat{Z}_1 e^{\lambda_1 t} + m_{12}\widehat{Z}_2 e^{\lambda_2 t}, \\
Z_2(t) &= m_{21}\widehat{Z}_1 e^{\lambda_1 t} + m_{22}\widehat{Z}_2 e^{\lambda_2 t},
\end{aligned}$$

where

$$\begin{aligned}
\lambda_3 &= a - \gamma > 0, \\
\lambda_1 &= \frac{1}{2}\left[(b-\varepsilon-\mu) + \sqrt{(b-\varepsilon-\mu)^2 + 4\Phi^2}\,\right] > 0, \\
\lambda_2 &= \frac{1}{2}\left[(b-\varepsilon-\mu) - \sqrt{(b-\varepsilon-\mu)^2 + 4\Phi^2}\,\right] < 0,
\end{aligned}$$

$(m_{11}, m_{21})^T$ and $(m_{12}, m_{22})^T$ are eigenvalues corresponding to λ_1 and λ_2, respectively. Clearly $(0,0,0,0)$ and $\big(N(t), P(t), Z_1(t), Z_2(t)\big)$ are a pair of lower and upper solutions of (2.5), (2.2) and (2.4). Thus, by Theorem 4.2 we have the following result.

Theorem 4.3. *If* $\lambda_3 = a - \gamma > 0$, *then there exists a unique solution of the* *initial and Neumann boundary value problem (2.5), (2.2) and (2.4), such that*

$$0 \le N(t,x) \le N(t),$$
$$0 \le P(t,x) \le P(t),$$
$$0 \le Z_1(t,x) \le Z_1(t),$$
$$0 \le Z_2(t,x) \le Z_2(t).$$

4.5 Periodic Solutions

Consider the general system

$$\frac{\partial u_j}{\partial t} - d_j \frac{\partial^2 u_j}{\partial x^2} + \sigma_j u_j = f_j(t,x,u),\ j = 1,2,\dots,n, \quad t \in (0,T), \quad x \in (0,a), \tag{5.1}$$

with the boundary value conditions

$$\left[-\alpha_{j1}\frac{\partial u_j}{\partial x} + \beta_{j1} u_j\right]_{x=0} = \gamma_{j1}(t), \quad \left[\alpha_{j2}\frac{\partial u_j}{\partial x} + \beta_{j2} u_j\right]_{x=a} = \gamma_{j2}(t),\ t \in [0,T], \tag{5.2}$$

where $u \equiv u(x,t) = (u_1,\dots,u_n)$, $d_j > 0$, $\sigma_j \ge 0$, $\alpha_{j\ell} \ge 0$, $\beta_{j\ell} \ge 0$ are constants on $D = (0,T)\times(0,a)$ with $\alpha_{j\ell} + \beta_{j\ell} > 0$ and $f_j, \gamma_{j\ell}$ are continuous functions of their respective arguments, $j = 1,2,\dots,n$, $\ell = 1,2$. Denote

$$L[u_j] = \frac{\partial u_j}{\partial t} - d_j \frac{\partial^2 u_j}{\partial x^2} + \sigma_j u_j,$$

and let λ_{jm} be the positive roots of the transcendental equation

$$\tan\ \lambda a = \frac{\lambda(h_{j1} + h_{j2})}{\lambda^2 - h_{j1}h_{j2}}, \quad j = 1,2,\dots,n \tag{5.3}$$

where

$$h_{j1} = \begin{cases} \frac{\beta_{j1}}{\alpha_{j1}}, & \alpha_{j1} \neq 0, \\ 0, & \alpha_{j1} = 0 \end{cases}, \qquad h_{j2} = \begin{cases} \frac{\beta_{j2}}{\alpha_{j2}}, & \alpha_{j2} \neq 0 \\ 0, & \alpha_{j2} = 0 \end{cases}$$

and $\varphi_j(\lambda_{jm}, x)$ is the corresponding eigenfunction

$$\varphi_j(\lambda_{jm}, x) = \frac{\lambda_{jm} \cos \lambda_{jm} x + h_{j1} \sin \lambda_{jm} x}{\Delta_m^{(j)}}, \tag{5.4}$$

where

$$\Delta_m^{(j)} = \left[\tfrac{1}{2}\,(\lambda_{jm}^2 + h_{j1}^2)(a + \frac{h_{j2}}{\lambda_{jm}^2 + h_{j2}^2} + \frac{h_{j1}}{2}\,)\right]^{1/2}.$$

The Green's function is given by

$$G_j(t - \tau, x, y) = \frac{1}{T} \sum_{m=1}^{\infty} \sum_{\rho=-\infty}^{\infty} \frac{\varphi_j(\lambda_{jm}, x)\varphi_j(\lambda_{jm}, y)}{\frac{2i\pi\rho}{T} + d_j \mu_{jm}^2} \cdot e^{\frac{2i\pi\rho}{T}(t-\tau)} \tag{5.5}$$

for $x,\ y \in (0, a),\quad t \neq \tau,\quad j = 1, 2, \ldots, n,\quad \mu_{jm} = \lambda_{jm}^2 + \frac{\sigma_j}{d_j}$. Define

$$g_j(t, x) = \frac{(x - a)^2 \gamma_{j1}(t)}{2a\alpha_{j1} + a^2 \beta_{j1}} + \frac{x^2 \gamma_{j2}(t)}{2a\alpha_{j2} + a^2 \beta_{j2}},$$

$$f_j^*(t, x, u) = f_j(t, x, u) - L[g_j].$$

Let $C(\overline{D})$ be the space of continuous T-periodic functions $V(t, x)$ on $\overline{D} = [0, T] \times [0, a]$ with the maximum norm $\|V\| = \max\,\{|V(t, x)| : (t, x) \in \overline{D}\}$ and let $\xi(\overline{D})$ be the product space $C(\overline{D}) \times \cdots \times C(\overline{D})$ equipped with the norm

$$\|V\| = \|V_1\| + \cdots + \|V_n\| \quad (V = (V_1, \ldots, V_n)).$$

Define an operator $\mathcal{A} : \xi(\overline{D}) \to \xi(\overline{D})$ by

$$\mathcal{A}u = (A_1 u, \ldots, A_n u) \quad (u \in \xi(\overline{D})),$$

where $A_j : \xi(\overline{D}) \to C(D)$ is the operator given by

$$(A_j u)(t,x) = \int_0^T d\tau \int_0^a G_j(t-\tau, x, y) f_j^*(\tau, y, u(\tau, y))dy + g_j(t,x).$$

For any constant $r > 0$, let $B_r = \{V \in \xi(\overline{D}) : \|V - V_0\| \leq r\}$, where $V_0 = \mathcal{A}\Theta$ and Θ is the zero function in $\xi(\overline{D})$.

Suppose there are a suitable pair of constants K^* and r such that f^* satisfies the following Lipschitz condition

$$|f^*(t_1, x, u_1) - f^*(t_2, x, u_2)| \leq K^*(|t_1 - t_2| + |u_1 - u_2|) \tag{5.6}$$

for $u_1, u_2 \in B_r$, $t, s \in [0,T]$ and $x \in [0,a]$.

We also make the following assumptions

(H_0) (i) For each $j = 1, 2, \ldots, n$, f_j is continuous, T-periodic with respect to t, and continuously differentiable with respect to (t, x, u) in $[0,T] \times [0,a] \times R^n$;

(ii) For each $j = 1, 2, \ldots, n$, $\ell = 1, 2$, the boundary data $\gamma_{j\ell}(t)$ are periodic and possess continuous second derivatives in $[0,T]$.

Now denote

$$M_1 = \sup\{|\varphi_j(\lambda_{jm}, x)| : 0 \leq x \leq a, \ j = 1, 2, \ldots, n, \ m = 1, 2, \ldots\} \tag{5.7}$$

$$M_2 = \sum_{j=1}^{n} \{\sum_{m=1}^{\infty} \frac{1}{d_j \mu_{jm}^2}\}. \tag{5.8}$$

We recall the following result due to Liu and Pao [17]

Lemma 5.1 ([17], Theorem 4). *Let* (H_0) *and (5.6) hold. If the constants* K^* *and* r *in (5.6) satisfy the relation*

$$\rho_0 = K^* M_1 M_2 \sqrt{a} < 1 \quad \text{and} \quad r \geq \rho_0 \, (1-\rho_0)^{-1} \|V_0\|,$$

then the boundary value problem (5.1), (5.2) has a unique T*-periodic solution in* B_r.

Denote

$$u = \begin{pmatrix} N \\ P \\ Z \end{pmatrix}, \qquad f(t,x,u) = \begin{pmatrix} f_1(t,x,u) \\ f_2(t,x,u) \\ f_3(t,x,u) \end{pmatrix},$$

where

$$\begin{aligned} f_1(t,x,u) &= -a\rho(t)\,\frac{NP}{k+N} + (1-\delta)bZ[1-e^{-\lambda(P-P_t)}] + \gamma P + \varepsilon Z, \\ f_2(t,x,u) &= a\rho(t)\,\frac{NP}{k+N} - bZ[1-e^{-\lambda(P-P_t)}] - \gamma P, \\ f_3(t,x,u) &= \delta b Z[1-e^{-\lambda(P-P_t)}] - \varepsilon Z. \end{aligned}$$

Clearly for each $j = 1,2,3$, $f_j(t,x,u)$ is continuous, 2θ-periodic with respect to t, continuously differentiable with respect to (t,x,u) in $[0,2\theta] \times [0,x_0] \times R^3$. Since

$$|\rho(t_1)\,\frac{N_1P_1}{k+N_1} - \rho(t_2)\,\frac{N_2P_2}{k+N_2}| \leq \frac{\pi}{2\theta}\,|\frac{N_1P_1}{k+N_1} - \frac{N_2P_2}{k+N_2}| + \frac{\pi^2 R_1}{2\theta^2}\,|t_1-t_2|$$

by the proof of Lemma 3.3, we have

$$|f_1(t_1,x,u_1) - f_1(t_2,x,u_2)| \leq \frac{a\pi^2 R_1}{2\theta^2}\,|t_1-t_2| + \Big(\frac{3a\pi}{2\theta} + \frac{2a\pi R_1}{k} + (1-\delta)b\lambda + \gamma\Big)|P_1-P_2|$$

$$+\left((1-\delta)b+\varepsilon\right)|Z_1-Z_2|,$$

$$|f_2(t_1,x,u_1)-f_2(t_2,x,u_2)| \le \frac{a\pi^2 R_1}{2\theta^2}\,|t_1-t_2| + \Big(\frac{3a\pi}{2\theta}+\frac{2a\pi R_1}{k}+b\lambda+\gamma\Big)|P_1-P_2|$$
$$+\, b|Z_1-Z_2|,$$

$$|f_3(t_1,x,u_1)-f_3(t_2,x,u_2)| \le (\delta b+\varepsilon)|Z_1-Z_2| + \delta b\lambda|P_1-P_2|.$$

Define

$$K^* = \max\{\frac{3a\pi}{2\theta}+\frac{2a\pi R_1}{k}+b\lambda+\gamma,\quad b+\varepsilon,\quad \frac{a\pi^2 R_1}{2\theta^2}\}. \tag{5.9}$$

Let $C(\overline{D})$ be the space of continuous 2θ-periodic functions $V(t,x)=(V_1,V_2,V_3)$ on $\overline{D}=[0,2\theta]\times[0,x_0]$ with the maximum norm $\|V\| = \max\ \{|V(t,x)| : (t,x)\in\overline{D}\}$, let $\xi(\overline{D})=\{C(\overline{D})\}^3$ with the norm

$$\|V\| = \|V_1\|+\|V_2\|+\|V_3\|.$$

Let $\mathcal{A}:\xi(\overline{D})\to\xi(\overline{D})$ be given by $\mathcal{A}u=(A_1u,A_2u,A_3u)$ where

$$(A_ju)(t,x) = \int_0^{2\theta} d\tau \int_0^{x_0} \frac{1}{2\theta}\sum_{m=1}^{\infty}\sum_{\rho=-\infty}^{\infty} \frac{\frac{2}{x_0}\sin\ \frac{m\pi x}{x_0}\sin\ \frac{m\pi y}{y_0}}{\frac{i\pi\rho}{\theta}+\frac{m^2\pi^2}{x_0^2}} e^{\frac{i\pi\rho}{\theta}(t-\tau)} f_j\big(\tau,y,u(\tau,y)\big)dy,$$

$j=1,2,3.$ For $r>0,$ define

$$B_r = \{V\in\xi(\overline{D}):\ \|V-V_0\|\le r\}, \tag{5.10}$$

where $V_0=\mathcal{A}\Theta$ and Θ is a zero function in $\{C(\overline{D})\}^3$. Since $\gamma_{j\ell}=0$ for $j=1,2,3$ and $\ell=1,2,$ $f^*=f,$ hence (5.6) holds in B_r.

Now $\alpha_{j\ell} = 0,\ \beta_{j\ell} = 1,\ d_j = 1,\ \sigma_j = 0$ for $j = 1,2,3$ and $\ell = 1,2$. The transcendental equation (5.3) is reduced to

$$\sin \lambda\, x_0 = 0 \quad (j = 1,2,3).$$

Hence $\lambda_{jm} = \frac{m\pi}{x_0}$ $(j = 1,2,3,\ m = 1,2,\dots)$, and the corresponding eigenfunctions have the form

$$\varphi_j(\lambda_{jm}, x) = \sqrt{\frac{2}{x_0}}\ \sin\ \frac{m\pi x}{x_0}\,, \quad j = 1,2,3, \quad m = 1,2,\dots\,.$$

Also

$$\begin{aligned} \mu_{jm} &= \lambda_{jm} = \frac{m\pi}{x_0}, \quad j = 1,2,3, \quad m = 1,2,\dots \\ M_1 &= \sup\,\{|\sqrt{\frac{2}{x_0}}\ \sin\ \frac{m\pi x_0}{x_0}| : j = 1,2,3, \quad m = 1,2,\dots\} = \sqrt{\frac{2}{x_0}}\,, \\ M_2 &= \sum_{j=1}^{3}\{\sum_{m=1}^{\infty} \frac{x_0^2}{m^2\pi^2}\} = \frac{x_0^2}{2\pi^2}\,. \end{aligned}$$

By Lemma 5.1 we have the following result.

Theorem 5.2. *If the constants* K^* *and* r *defined by (5.9) and (5.10) satisfy the relation*

$$K^* < \frac{\sqrt{2}\,\pi^2}{x_0^2} \quad \text{and} \quad r \geq \frac{\|V_0\|}{\frac{\sqrt{2}\,\pi^2}{K^* x_0^2} - 1}\,,$$

then the Dirichlet boundary value problem (2.6) and (2.7) has a unique 2θ*-periodic solution in* B_r.

4.6 Discussion

We have discussed reaction-diffusion models of zooplankton-phytoplankton-nutrient interactions with instantaneous nutrient recycling. Due to the nutrient recycling terms, our models are different from the reaction-diffusion simple food-chain model (Kuang [13]) and the diffusion chemostat-type models (So and Waltman [29], Waltman [32]).

We have studied the global existence and global stability of solutions of a model under initial value conditions and Dirichlet boundary value conditions by a semigroup approach. For the Neumann initial-boundary value problem, a comparison theorem is established for the existence of solutions.

Periodicities have also been included into our considerations. Periodic terms are an approximation to natural oscillations of carrying capacities (seasons, weather, etc.) and even in the boundary conditions (tidal effects). Hence we have also considered a reaction-diffusion model with periodic coefficients. It is shown that there is a unique periodic solution for the Dirichlet boundary value problem.

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CHAPTER 5

AN INTEGRODIFFERENTIAL MODEL

5.1 Introduction

Recently, Beretta, Bischi and Solimano [1] studied a chemostat-type model to simulate the growth of planktonic communities of unicellular algae in lakes, where the plankton feeds on a limiting nutrient supplied at a constant rate. They supposed that the limiting nutrient is partially recycled after the death of the organisms and they used a distributed delay to model the nutrient recycling in order to study its effect on the stability of the positive equilibrium. In [2], Bischi investigated the effects of the time delay involved in nutrient recycling on resilience, that is, the rate at which a system returns to a stable steady state following a perturbation. Their results show that when a system is characterized by oscillatory behavior, an increase in the distributed time delay can have a stabilizing effect. This is a counterintuitive result, because in general it has been found that the introduction of time delays is a destabilizing process, in the sense that increasing the time delay could cause a stable equilibrium to become unstable and/or cause the populations to fluctuate (see Cushing [8], Freedman and Rao [9], Gopalsamy and Aggarwala [13], MacDonald [20]).

The mathematical analysis of chemostat-type models has been studied by many authors. In the case of instantaneous dynamics, we refer to a recent survey paper by Waltman [25] and the references cited therein. Chemostat-type models incorporating discrete delays have been investigated by Freedman, So and Waltman [10]. We refer to Cushing [8], Gopalsamy [11, 12] and MacDonald [20] for further references to delayed models in population biology.

In this chapter, we introduce a discrete time delay term to the model of

Beretta, Bischi and Solimano [1], this term may be considered as delay due to gestation, and we also allow the washout rates for nutrient and plankton to be different. By using the "linear chain trick technique" of MacDonald [20], we can transform the two dimensional integrodifferential system to a three dimensional one with a discrete time delay. Using the discrete time delay as a bifurcation parameter, we show that the model undergoes a Hopf bifurcation. We also consider the question of persistence of the model. It is shown that conditions for uniform persistence are the same as those for the instantaneous case. Hence both the discrete time delay and the distributed time delay are "harmless" (a term coined by Gopalsamy [11]) in our model.

We now recall the definitions of persistence given in Butler, Freedman and Waltman [4]. A component $x(t)$ of a given ODE system is said to be ***persistent*** if for any $x(0) > 0$ it follows that $x(t) > 0$, $t > 0$ and $\liminf\limits_{t\to\infty} x(t) > 0$. If there exists $\delta > 0$ (independent of $x(0)$) such that $x(t)$ is persistent and $\liminf\limits_{t\to\infty} x(t) > \delta$, then $x(t)$ is said to be ***uniformly persistent***. For a FDE system, a component $x(t)$ is persistent if for any $\phi(s) > 0$, $-\infty < s < t_0$, it follows that $x(t) > 0$, $t > 0$ and $\liminf\limits_{t\to\infty} x(t) > 0$. If there exists $\delta > 0$ (independent of $\phi(t)$) such that $x(t)$ is persistent and $\liminf\limits_{t\to\infty} x(t) > \delta$, then $x(t)$ is said to be ***uniformly persistent***. A system is uniformly persistent if each component is uniformly persistent.

A system is dissipative if for any solution $y(t)$, there is a positive number M such that $\limsup\limits_{t\to\infty} |y(t)| < M$. To verify this property for a given system, usually Liapunov functions (functionals) and differential inequalities are employed. We refer readers interested in appropriate techniques to a recent paper by Haddock et al [14] on functional differential equations with infinite delay.

The rest of this chapter is organized as follows. In Section 5.2 the integrodifferential model with a discrete time delay and a distributed time delay is described. We will review some previous results on some special cases of our model in Section 5.3. In Section 5.4 we prove that the system is dissipative and that a Hopf bifurcation occurs at the positive equilibrium if the discrete delay is increased past a critical value. Persistence is also discussed in this section. Finally, some concluding remarks and discussions are given in Section 5.5.

5.2 The Model

We consider the following integrodifferential system as a model of plankton-nutrient interaction with a discrete time delay due to gestation and a distributed time delay involved in nutrient recycling

$$\begin{aligned} \frac{dN}{dt} &= D(N^0 - N) - aPu(N) + \gamma_1 \int_{-\infty}^{t} F(t-s)P(s)ds \\ \frac{dP}{dt} &= P[a_1 u(N(t-\tau)) - (\gamma + D_1)] \end{aligned} \tag{2.1}$$

with initial conditions

$$N(s) = \phi(s), \quad s \in [-\tau, 0],$$

$$P(s) = \psi(s), \quad s \in (-\infty, t_0],$$

where N is the concentration of a limiting nutrient and P is a measure of plankton population.

In system (2.1), all parameters are positive constants. D is the washout rate of nutrient, $\frac{1}{D}$ has the physical dimension of a time and represents the average time that nutrient and waste products spend in the system (see Smith [24]). D_1

is the washout rate of plankton, and we assume that $D \neq D_1$ (see Wolkowicz and Lu [28] and Ruan [23]). N^0 is the input concentration of the limiting nutrient, a is the maximum uptake rate of nutrient and $a_1(\leq a)$ is the maximum specific growth rate of plankton, γ is the death rate of plankton and $\gamma_1(\leq \gamma)$ is the nutrient recycled rate after the death of plankton. There is a delay of time τ due to gestation, we model which following Bush and Cook [5].

The function $u(N)$ describes the nutrient uptake rate of plankton. We assume the following general hypotheses on $u(N)$ (see Hale and Somolinos [15]).

(i) $u(N)$ is non-negative, increasing and vanishes when there is no nutrient;

(ii) there is a saturation effect when the nutrient is very abundant.

That is, $u(N)$ is a continuous function defined on $[0, \infty)$ and

$$u(0) = 0, \quad \frac{du}{dN} > 0, \quad \lim_{N \to \infty} u(N) = 1.$$

In particular, these hypotheses are satisfied by the Michaelis-Menten function (Caperon [6])

$$u(N) = \frac{N}{k+N},$$

where $k > 0$ is the half-saturation constant or Michaelis-Menten constant.

The delay-kernel $F(s)$ is a non-negative bounded function defined on $[0, \infty)$ and describes the contribution of the plankton population dead in the past to the nutrient recycled at time t. The presence of the distributed time delay must not affect the equilibrium values, so we normalize the kernel such that

$$\int_0^\infty F(s)ds = 1. \tag{2.2}$$

According to MacDonald [20], we define the average time lag as

$$T = \int_0^\infty sF(s)ds. \tag{2.3}$$

In particular, the exponential kernal

$$F(s) = \alpha e^{-\alpha s}, \ \alpha > 0 \tag{2.4}$$

is usually used (see Cushing [8], Cunningham and Nisbet [7]); the average time lag is

$$T = \int_0^\infty se^{-\alpha s}ds = \frac{1}{\alpha}.$$

Note that $E_0 = (N^0, 0)$ is always an equilibrium for system (2.1), and if

$$\gamma + D_1 < a_1 \quad \text{and} \quad u^{-1}(\frac{\gamma + D_1}{a_1}) < N^0, \tag{2.5}$$

system (2.1) has a positive interior equilibrium $E^* = (N^*, P^*)$ with

$$N^* = u^{-1}(\frac{\gamma + D_1}{a_1}), \quad P^* = \frac{a_1 D(N^0 - N^*)}{a(\gamma + D_1) - a_1\gamma_1}. \tag{2.6}$$

5.3 Some Special Cases

In this section we consider some special cases of system (2.1).

Case I. $\tau = 0$, $F(s) = \delta(s)$.

When the time delays are neglected, that is, the discrete delay $\tau = 0$ and the delay kernel is a delta function $F(s) = \delta(s)$, we get the following instantaneous model

$$\begin{aligned}\frac{dN}{dt} &= D(N^0 - N) - aPu(N) + \gamma_1 P \\ \frac{dP}{dt} &= P[a_1 u(N) - (\gamma + D_1)].\end{aligned} \tag{3.1}$$

Model (3.1) was studied by Beretta, Bischi and Solimano [1] and Ruan [23]. According to Theorem 2.6 of [23], we first have the following

Proposition 3.1. *System (3.1) is dissipative.*

System (3.1) has the same equilibria E_0 and E^* as system (2.1). By Theorem 3.1 of [1], we have

Proposition 3.2. *If* $u(N^0) < \dfrac{\gamma + D_1}{a_1}$, *then* $\lim_{t\to\infty}(N(t), P(t)) = E^0$.

This result indicates that if the maximum growth rate of the plankton population is less than or equal to its loss rate, i.e. $a_1 \le \gamma + D_1$, or the plankton population does not have enough nutrient, i.e. $a_1 > \gamma + D_1$ but $u(N^0) < \dfrac{\gamma + D_1}{a_1}$, then the plankton population becomes extinct.

By Theorem 3.2 of [1], we have

Proposition 3.3. *If the positive equilibrium* E^* *exists, it is globally asymptotically stable in* R^2_+.

Comparing to the results in chemostat models in Waltman, Hubbell and Hsu [26], we can see that the nutrient recycling term plays a stablizing role for the positive equilibrium. Since possessing a globally asymptotically stable equilibrium is sufficient for persistence, we have the following

Proposition 3.4. *If the inequalities in (2.5) hold, then system (3.1) is uniformly persistent.*

Propositions 3.3 and 3.4 show that if the maximum growth rate of plankton is greater than its loss rate and plankton has enough nutrient, then the plankton population has long term survival.

Case II. $F(s) = \delta(s)$.

When the distributed time delay in the nutrient recycling term is neglected, i.e. $F(s) = \delta(s)$, model (2.1) becomes

$$\begin{aligned} \frac{dN}{dt} &= D(N^0 - N) - aPu(N) + \gamma_1 P \\ \frac{dP}{dt} &= P[a_1 u(N(t-\tau)) - (\gamma + D_1)]. \end{aligned} \tag{3.2}$$

This model also has the same equilibria E_0 and E^* as system (2.1) if the inequalities in (2.5) hold. A similar chemostat type model was studied by Freedman, So and Waltman [10]. Analogous to the procedures in [10], one can prove the following results.

Proposition 3.5. *System (3.2) is dissipative.*

Proposition 3.6. *There exists $\tau_0 > 0$ such that a family of periodic solutions of system (3.2) bifurcates from E^* for τ near τ_0.*

Similar to the proof of Theorem 5.5 of Zhao [29], we can prove the following persistence result about the discrete delay model.

Proposition 3.7. *If the inequalities in (2.5) hold, then system (3.2) is uniformly persistent.*

Case III. $\tau = 0$.

When the discrete time delay due to gestation is neglected, i.e. $\tau = 0$, the model has the following form

$$\begin{aligned} \frac{dN}{dt} &= D(N^0 - N) - aPu(N) + \gamma_1 \int_{-\infty}^{t} F(t-s)P(s)ds \\ \frac{dP}{dt} &= P[a_1 u(N) - (\gamma + D_1)]. \end{aligned} \tag{3.3}$$

Again system (3.3) has the same equilibria E_0 and E^* as system (2.1) provided the inequalities in (2.5) are satisfied. System (3.3) was studied by Beretta, Bischi and Solimano [1] and Bischi [2]. By Theorem 2.1 of [1] or Theorem 1 of [2], we have

Proposition 3.8. *System (3.3) is dissipative.*

Similar to Theorems 4.1 and 4.2 in [1], we have the following stability criteria independent of the value of distributed time delay.

Proposition 3.9. *If*

$$(D + aP^*u'(N^*))^2 \geq 2aP^*u'(N^*)(\gamma + D_1),$$

then the positive equilibrium E^* of system (3.3) is locally asymptotically stable. In particular, if $F(s) = \alpha e^{-\alpha s}$, then E^* is always asymptotically stable.

5.4 Hopf Bifurcation and Persistence

From now on, we suppose $F(s) = \alpha e^{-\alpha s}$ for $\alpha > 0$, i.e. we consider the following model

$$\begin{aligned}\frac{dN}{dt} &= D(N^0 - N) - aPu(N) + \gamma_1 \int_{-\infty}^{t} \alpha e^{-\alpha(t-s)} P(s)ds \\ \frac{dP}{dt} &= P[a_1 u(N(t-\tau)) - (\gamma + D_1)].\end{aligned} \tag{4.1}$$

The following result shows that solutions of system (4.1) are bounded and hence lie in a compact set and are continuable for all positive time.

Theorem 4.1. *System (4.1) is dissipative.*

PROOF: We choose

$$V(t, N(t), P(\cdot)) = N(t) + \frac{a}{a_1}P(t) + \gamma_1 \int_{-\infty}^{t} \int_{t-s}^{\infty} \alpha e^{\alpha\xi} d\xi P(s)ds.$$

The derivative of V along the trajectories of (4.1) is

$$\begin{aligned}\frac{dV}{dt} &= D(N^0 - N) - aPu(N) + \gamma_1 \int_{-\infty}^{t} \alpha e^{-\alpha(t-s)} P(s)ds \\ &\quad + aPu(N(t-\tau)) - \frac{\gamma + D_1}{a_1}P \\ &\quad + \gamma_1 P \int_{0}^{\infty} \alpha e^{\alpha\xi} d\xi - \gamma_1 \int_{-\infty}^{t} \alpha e^{-\alpha(t-s)} P(s)ds \\ &= D(N^0 - N) - \frac{\gamma + D_1 - \gamma_1 a_1}{a_1}P \\ &\quad - aP[u(N(t)) - u(N(t-\tau))] \\ &\le -DN - \frac{\gamma + D_1 - \gamma_1 a_1}{a_1}P + DN^0\end{aligned}$$

if $N(\xi) \leq N(t)$ for $t-\tau \leq \xi \leq t$. By a classical Liapunov- Razumikhin theorem about boundedness (see, c.f. Haddock et al [14]), we know that system (4.1) is dissipative. This completes the proof.

Now we define a new variable

$$Y(t) = \int_{-\infty}^{t} \alpha e^{-\alpha(t-s)} P(s) ds, \tag{4.2}$$

then by the linear chain trick technique (MacDonald [20]), the two dimensional integrodifferential system (4.1) can be transformed into an equivalent three dimensional one with a discrete delay

$$\begin{aligned} \frac{dN}{dt} &= D(N^0 - N) - aPu(N) + \gamma_1 Y \\ \frac{dP}{dt} &= P[a_1 u(N(t-\tau)) - (\gamma + D_1)] \\ \frac{dY}{dt} &= \alpha P - \alpha Y, \end{aligned} \tag{4.3}$$

where the variable $Y(t)$ can be interpreted as an intermediate component which causes the delay, such as the dead plankton in the sediments.

System (4.3) has two equilibria provided the inequalities in (2.5) hold. If confusion does not arise, they are still denoted by $E_0 = (N^0, 0, 0)$ and $E^* = (N^*, P^*, Y^*)$ with $P^* = Y^*$.

The linearized system of (4.3) at the equilibrium E^* has the form

$$\begin{aligned} \frac{dn(t)}{dt} &= -(D + aP^* u'(N^*))n(t) - au(N^*)p(t) + \gamma_1 y(t) \\ \frac{dp(t)}{dt} &= a_1 P^* u'(N^*) n(t-\tau) \\ \frac{dy(t)}{dt} &= \alpha p(t) - \alpha y(t), \end{aligned} \tag{4.4}$$

where $n(t) = N(t) - N^*$, $p(t) = P(t) - P^*$ and $y(t) = Y(t) - Y^*$. This leads to the characteristic equation

$$\lambda^3 + \rho\lambda^2 + \beta\lambda = \delta e^{-\lambda\tau} + \eta\lambda e^{-\lambda\tau}, \tag{4.5}$$

where

$$\begin{aligned}
&\rho = \alpha + D + aP^*u'(N^*) > 0,\\
&\beta = \alpha(D + aP^*u'(N^*)) > 0,\\
&\delta = -\alpha a_1 P^*u'(N^*)(au(N^*) - \gamma_1) < 0,\\
&\eta = -aa_1 P^*u(N^*)u'(N^*) < 0.
\end{aligned}$$

The stability of E^* can be determined according to the sign of the real parts of the solutions λ of equation (4.5). Let $\lambda = \mu + i\nu$, we consider λ and hence μ and ν as functions of the delay τ. Substituting into (4.5), we obtain the following equations

$$\begin{aligned}
\mu^3 - 3\mu\nu^2 + \rho(\mu^2 - \nu^2) + \beta\mu &= \left[(\delta + \eta\mu)\cos\tau\nu + \eta\nu\sin\tau\nu\right]e^{-\tau\mu},\\
-\nu^3 + 3\mu^2\nu + 2\rho\mu\nu + \beta\nu &= \left[\eta\nu\cos\tau\nu - (\delta + \eta\mu)\sin\tau\nu\right]e^{-\tau\mu}.
\end{aligned} \tag{4.6}$$

A necessary condition for a stability change of E^* is that the characteristic equation has a pure imaginary solution $\lambda = i\nu$. Let $\hat{\tau}$ be such that $\mu(\hat{\tau}) = 0$. Then we can reduce equations (4.6) to (where $\hat{\nu} = \nu(\hat{\tau})$)

$$\begin{aligned}
-\rho\hat{\nu}^2 &= \delta\cos\hat{\tau}\hat{\nu} + \eta\hat{\nu}\sin\hat{\tau}\hat{\nu},\\
-\hat{\nu}^3 + \beta\hat{\nu} &= \eta\hat{\nu}\cos\hat{\tau}\hat{\nu} - \delta\sin\hat{\tau}\hat{\nu}.
\end{aligned} \tag{4.7}$$

Equations (4.7) give an equation in $\hat{\nu}$ of the form

$$\Phi(\hat{\nu}^2) = \hat{\nu}^6 + (\rho^2 - 2\beta)\hat{\nu}^4 + (\beta^2 - \eta^2)\hat{\nu}^2 - \delta^2 = 0. \tag{4.8}$$

Since when $\hat{\nu} = 0$, $\Phi(0) < 0$ and for sufficiently large values of $\hat{\nu}$, $\Phi > 0$, hence the cubic equation (4.8) has one or more real roots $\hat{\nu}^2$. From equations (4.7), we can solve for $\hat{\tau}$, which is

$$\hat{\tau}_n = \frac{1}{\hat{\nu}} \arcsin \frac{\hat{\nu}^3(\delta - \rho\eta) - \hat{\nu}\beta\delta}{\eta^2\hat{\nu}^2 + \delta^2} + \frac{2n\pi}{\hat{\nu}}, \qquad n = 0, 1, 2, \ldots. \tag{4.9}$$

In order to establish Hopf bifurcation at $\tau = \hat{\tau}$, we need to show that $\frac{d}{d\tau}\mu(\hat{\tau}) \neq 0$. From (4.6), differentiating with respect to τ and setting $\tau = \hat{\tau}$, $\nu = \hat{\nu}$, $\mu = 0$, and solving for $\frac{d\mu}{d\tau}$ and $\frac{d\nu}{d\tau}$, we get

$$\frac{d\mu(\hat{\tau})}{d\tau} = \frac{AC - BD}{A^2 + B^2}, \tag{4.10}$$

where

$$A = 3\hat{\nu}^2 - \beta - \eta\hat{\tau}\hat{\nu}\sin\hat{\tau}\hat{\nu} + (\eta - \delta\hat{\tau})\cos\hat{\tau}\hat{\nu},$$

$$B = 2\rho\hat{\nu} + (\eta - \delta\hat{\tau})\sin\hat{\tau}\hat{\nu} + \eta\hat{\tau}\hat{\nu}\cos\hat{\tau}\hat{\nu},$$

$$C = \delta\hat{\tau}\sin\hat{\tau}\hat{\nu} - \eta\hat{\nu}^2\cos\hat{\tau}\hat{\nu},$$

$$D = \eta\hat{\nu}^2\sin\hat{\tau}\hat{\nu} + \delta\hat{\nu}\cos\hat{\tau}\hat{\nu}.$$

Using (4.7), we have

$$\begin{aligned} AC - BD &= \hat{\nu}^2[3\hat{\nu}^4 + 2(\rho^2 - 2\beta)\hat{\nu}^2 + (\beta^2 - \eta^2)] \\ &= \hat{\nu}^2 \frac{d\Phi}{d\hat{\nu}^2}. \end{aligned}$$

Hence if $\hat{\nu}_0$ is the first positive root of (4.8), we have

$$\frac{d\mu(\hat{\tau}_0)}{d\tau} = \frac{\hat{\nu}_0^2}{A^2 + B^2} \frac{d\Phi}{d\hat{\nu}^2}(\hat{\nu}_0^2) > 0,$$

where

$$\hat{\tau}_0 = \frac{1}{\hat{\nu}_0} \arcsin \frac{\hat{\nu}_0^3(\delta - \rho\eta) - \hat{\nu}_0\beta\delta}{\eta^2\hat{\nu}_0^2 + \delta^2}.$$

By the Hopf Bifurcation theorem (see, c.f. [21] or [17]), we have the following

Theorem 4.2. *A Hopf bifurcation occurs from* E^* *for* τ *near* $\hat{\tau}_0$.

As an example, let $u(N)$ be the Michaelis-Menten uptake function. We consider the system

$$\begin{aligned} \frac{dN}{dt} &= 0.1(20 - N) - \frac{10NP}{6+N} + 3.2\int_{-\infty}^{t} 0.2e^{-0.2(t-s)}P(s)ds \\ \frac{dP}{dt} &= P[\frac{9N(t-\tau)}{6+N(t-\tau)} - 4.1)]. \end{aligned} \tag{4.11}$$

If $\tau = 0$, with the same parameters the numerical simulations of Beretta, Bischi and Solimano [1] suggest that the positive equilibrium is "practically " globally stable.

We choose $\tau = 0.41$, the Hopf bifurcation is graphically illustrated as follows.

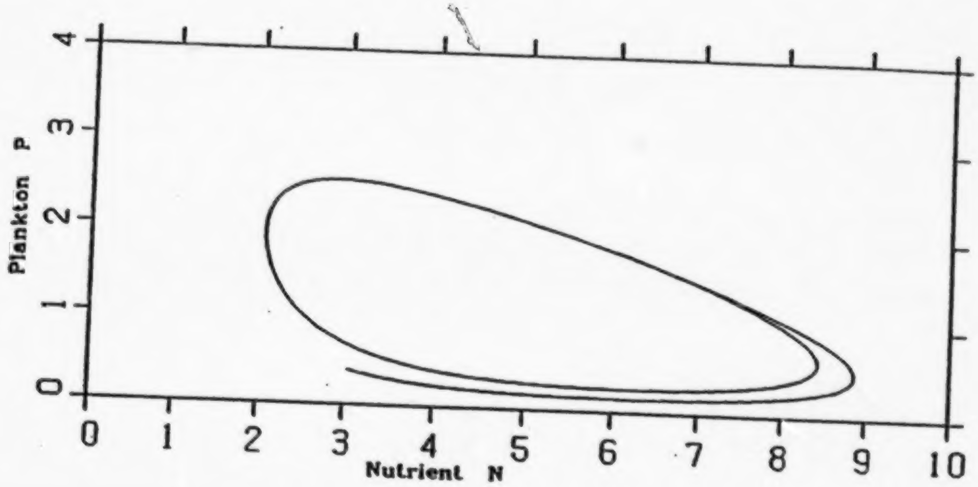

Fig. V Hopf bifurcation.

We know that E_0 is the only boundary equilibrium of system (4.3). At E^0 the characteristic equation has the form

$$(\lambda + D)(\lambda + \alpha)[\lambda - (a_1 u(N^0) - (\gamma_1 + D_1))] = 0. \tag{4.12}$$

It follows that two of the eigenvalues $\lambda_1 = -D$ and $\lambda_2 = -\alpha$ are negative. If the inequalities in (2.5) hold, then the third eigenvalue $\lambda_3 = a_1 u(N^0) - (\gamma_1 + D_1)$ is positive. Also, in a sufficiently small half- disc neighbourhood of E^0, $\frac{dP}{dt}$ is positive by the second equation of system (4.3), so there is no trajectory approaching E_0 from the P direction. Hence E_0 is locally stable in the N and Y directions and is locally unstable in the P direction, that is, E_0 is a saddle point. Solutions initiating on the $N-$ axis tend to E_0 and the stable set of E_0 does not intersect the positive cone. Hence E_0 is the only compact invariant set on the boundary, and there are no cycles in the boundary.

Therefore, according to the main theorem of Hale and Waltman [16], we have the following result.

Theorem 4.3. *If the inequalities in (2.5) hold, then system (4.3) and hence system (4.1) is uniformly persistent.*

Note that by Proposition 3.4 the inequalities in (2.5) are also persistence conditions for the instantaneous model (3.1).

5.5 Discussion

We have considered a plankton-nutrient model with a discrete time delay and a distributed time delay. The discrete time delay is regarded as the the lag due to gestation and the distributed time delay is used to described the nutrient recycling.

We have studied the boundedness of solutions of the model. By choosing the discrete delay as a bifurcation parameter, we have shown that a Hopf bifurcation may occur when the discrete delay passes its critical value. This is parallel to the case with only a discrete time delay (Proposition 3.6). Note that in the case with only a distributed time delay, Hopf bifurcation does not occur (Beretta, Bischi and Solimano [1]). Our result shows that the effect of the discrete time delay on the model is somehow stronger than that of the distributed time delay.

We have also investigated persistence of the model. It is interesting that the conditions for uniform persistence are the same as that for the instantaneous model (Proposition 3.4 and Theorem 4.3), which are also the same conditions for existence of a positive equilibrium. The first equivalent can be explained as that both the discrete time delay and the distributed time delay are "harmless" for persistence in our model. Similar phenomena have been observed by Wang and Ma [27] for models with discrete time delay, and by Burton and Hutson [3] for models with continuous (infinite) delay. Even through the stability of the interior equilibrium can not be determined in our model, our result shows that existence conditions of the interior equilibrium are enough to ensure uniform persistence of the model.

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CHAPTER 6

CONCLUDING DISCUSSION AND REMARKS

In this thesis we have studied the dynamics of several plankton models with nutrient recycling. The models were described by ordinary differential equations, reaction-diffusion equations and integrodifferential (delay) equations and the nutrient recycling was instantaneous as well as delayed.

In Chapter 2, we have discussed several zooplankton-phytoplankton-nutrient models with general nutrient uptake functions and instantaneous nutrient recycling terms. As opposed to the models studied by Wroblewski et al. [9] and Busenberg et al. [3], we introduced a nutrient concentration input and washout rates to the plankton-nutrient interacting models.

In the first instance, we have considered a model with a constant nutrient input and different constant washout rates. Further, the zooplankton population could be facultative or obligate. We have given conditions for boundedness of solutions, existence and stability of the equilibria and persistence criteria for the system. Competition for the nutrient exists in some sense if zooplankton is facultative, but the competitive exclusion principle does apply here. For the case where the zooplankton is obligate, persistence has been studied.

We have also considered the plankton-nutrient interacting models with periodic nutrient input and periodic washout rate, respectively. In both cases, there are positive periodic solutions in the three dimensional spaces bifurcating from stable periodic solutions in the $N-P$ plane with the death rate of zooplankton used as a bifurcating parameter. Hence coexistence of all three components occurs.

In Chapter 3, we have considered a three-trophic-level model of plankton dynamics with instantaneous nutrient recycling, which consists of autotrophic phytoplankton, herbivorous zooplankton, carnivorous zooplankton and dissolved limiting nutrient. We supposed that there are constant inputs concentration to the system and a constant washout rates from the system.

First we gave criteria for autotrophic phytoplankton or herbivorous zooplankton or carnivorous zooplankton or all of them to become extinct. The extinction results implied that bifurcation can occur. Since a predator-prey system can have an oscillatory tendency, it is natural to seek oscillatory coexistence of all elements of the population. Next we have studied the questions of persistence. Sufficient conditions were given which guarantee the survival of all elements of the population, which also imply the existence of an interior equilibrium in the positive cone.

Finally, under appropriate circumstances, a bifurcation theorem was used to show that coexistence of the autotroph, herbivore and carnivore occurs in the form of a bifurcating periodic orbit.

In Chapter 4, we have discussed reaction-diffusion models of zooplankton-phytoplankton-nutrient interactions with instantaneous nutrient recycling. Due to the nutrient recycling terms, our models are different from the reaction-diffusion simple food-chain model (Kuang [5]) and the diffusion chemostat-type models (So and Waltman [6], Waltman [7]).

We have studied the global existence and global stability of solutions of a model under initial value conditions and Dirichlet boundary value conditions by a semigroup approach. For the Neumann initial-boundary value problem, a comparison theorem was established for the existence of solutions.

Periodicities have also been included into our considerations. Periodic terms are an approximation to natural oscillations of carrying capacities (seasons, weather, etc.) and even in the boundary conditions (tidal effects). Hence we have also considered a reaction-diffusion model with periodic coefficients. It is shown that there was a unique periodic solution for the Dirichlet boundary value problem.

In Chapter 5, we have considered a plankton-nutrient model with a discrete time delay and a distributed time delay. The discrete time delay was regarded as the the lag due to gestation and the distributed time delay was used to describe the nutrient recycling.

We have studied the boundedness of solutions of the model. By choosing the discrete delay as a bifurcation parameter, we have shown that a Hopf bifurcation may occur when the discrete delay passes its critical value. This is parallel to the case with only a discrete time delay (Proposition 3.6). Note that in the case with only a distributed time delay, Hopf bifurcation does not occur (Beretta, Bischi and Solimano [1]). Our result shows that the effect of the discrete time delay on the model is somehow stronger than that of the distributed time delay. An example was also given to illustrate the obtained results.

We have also investigated persistence of the model. It is interesting that the conditions for uniform persistence are the same as that for the instantaneous model (Proposition 3.4 and Theorem 4.3), which are also the same conditions for existence of a positive equilibrium. The first equivalent can be explained as follows: that both the discrete time delay and the distributed time delay are "harmless" for persistence in our model. Similar phenomena have been observed by Wang and Ma [8] for models with discrete time delay (see also Freedman and Ruan [4]), and by Burton and Hutson [2] for models with continuous (infinite) delay. Even through the stability of the interior equilibrium can not be determined in our model, our result shows that existence conditions of the interior equilibrium are enough to ensure uniform persistence of the model.

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